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ANIMAL BEHAVIOR AND INTERNAL DRIVES

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ONE of the most fundamental of all the phenomena which characterize animal life and distinguish it from plant life is the spontaneous motility of the animal organism. A few plants, to be sure, especially certain forms of marine vegetation, do move about, but these few are exceptions in the plant kingdom. The activity of animals, on the other hand, although it varies widely in form and extent from species to species, is an ordinary phenomenon which one always anticipates under normal circumstances. We may ask, then, what it is that sets off the diverse performances which animals display. Ordinarily we think of most of their activity as being due to some form of external stimulation. We know, however, that all animals, from the lowest uni-cellular organism to man, are active even when all external stimuli have been eliminated. And since this spontaneous motility, just as any other kind of motility, must have a definite cause, it must be due to some natural factor within the organism. Many workers have chosen to call it "voluntary" activity, presumably because of the common belief that the "will" to do is the origin of the action. We believe, however, that spontaneous activity arises from certain underlying physiological origins. We shall attempt to show from studies chiefly on the white rat what some of these origins are, and how they fit into the general biological picture of the animal's life.

The investigations described below have been made by Ging H. Wang, Elaine F. Kinder, Tomi Wada, and the present writer in the Psychobiological Laboratory of the Phipps Psychiatric Clinic during the past six years. Some of the experiments have already been reported elsewhere, but we have taken this opportunity to collect also numerous observations that are as yet unpublished. Of the extensive work on animal "drives" done by Hoskins (1925), Moss (1924), Slonaker (1924, 1925, 1926), Stone (1924, 1925, 1926), Szymanski (1920, 1922), and Tracy (1926) we shall incorporate in this review only that part which bears directly on our own method of approach or on our own experimental findings.

PERIODIC NATURE OF SPONTANEOUS ACTIVITY—TWO-HOUR RHYTHM

We may begin our review with the rat confined just after feeding in a small cage

of the type shown in figure 1. The walls and floor of the cage are absolutely bare and the room in which the experiment is performed is kept constantly illuminated and free from all disquieting noises and odors. If we observe the animal for a while we see that it moves about most of the time, doing many things. It sniffs and claws at the walls of the cage, it climbs, and gnaws and scratches; but from all these observations, however interesting at first sight, we learn nothing of what makes it active. If, however, we arrange the cage so that every movement therein, even the slightest, is recorded over a period of ten to twelve hours on a smoked drum, a remarkable fact comes to light: this diffuse gross bodily activity occurs rhythmically, active periods alternating with periods of almost complete quiescence. The active periods occur at intervals varying from one to two hours. Moreover, the records show further that the activity within each active period is slight at the beginning, but increases as the period advances and reaches its maximum usually near the end (Richter, 1922). Typical records obtained from two rats in triangular cages are shown in figure 2. The record in figure 3, obtained from a guinea pig in the same type of cage, is representative of a similar rhythm found in other animals.

Had the motility been irregular and non-periodic we should have accomplished nothing in our investigation of its origin. On the contrary, however, it is very significant that such well defined periods of activity, recurring at such regular intervals, are found when external conditions are as nearly constant as is practically possible. This fact would indicate that the motility rhythm must be set up from within the animal in some organ which functions at a similar frequency of one and a half to two hours.

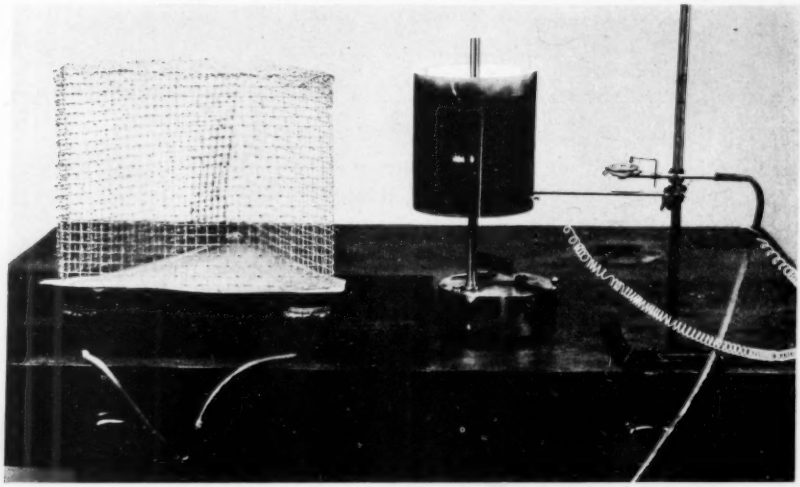

FIG. 1. PHOTOGRAPH OF CAGE USED IN STUDYING GROSS BODILY ACTIVITY

The cage is triangular in shape, 12 inches high and 12 inches wide. Each corner is supported on a rubber tambour through which all movements are transmitted to a recording Marey tambour. The time is recorded on the smoked paper in half hour intervals by means of an eight day clock.

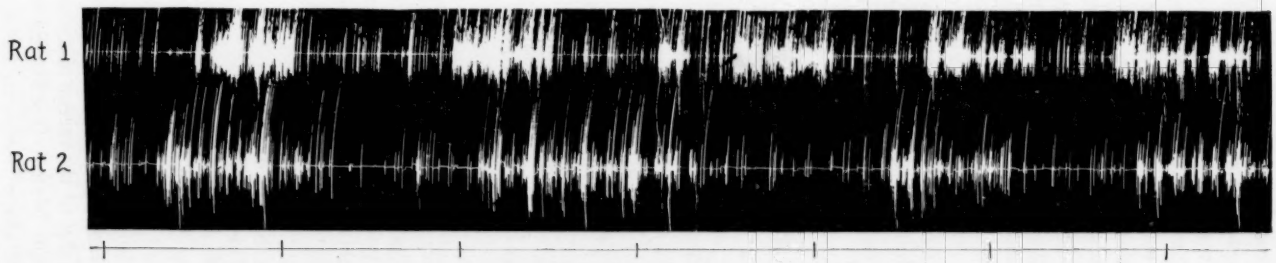

FIG. 2. RECORDS FROM TWO ADULT RATS SHOWING THE PERIODIC NATURE OF THEIR SPONTANEOUS ACTIVITY
Time is given in hours below the record

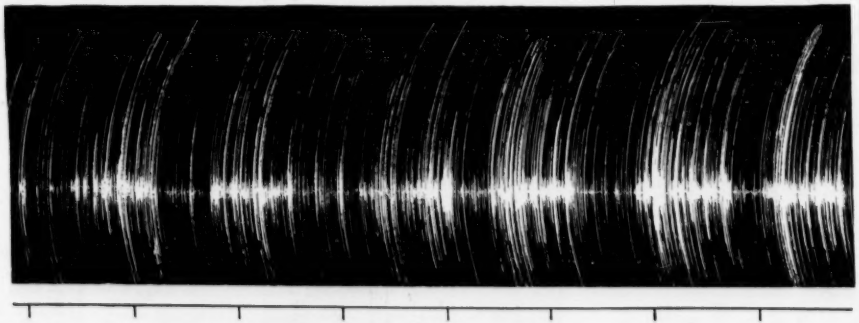

FIG. 3. RECORD OF SPONTANEOUS ACTIVITY OF AN ADULT GUINEA PIG
Time in hours below the record

ORIGIN OF THE TWO-HOUR-ACTIVITY RHYTHM

A review of the periodicity of the different viscera eliminates at once the heart and lungs and the sex glands, since the two former organs function at a frequency much higher and the latter at a frequency much lower than that of the bodily activity rhythm. In the stomach, however, we know that active periods alternate with quiescent intervals every hour and a half to two hours. In 1904 Boldireff was able to show that contractions occur in the walls of the empty stomach, but several years elapsed before Carlson (1916) demonstrated the periodic nature of this activity. Carlson, working with guinea pigs, dogs, and monkeys, found that from one to two hours after a meal, when the stomach is nearly empty, contraction waves begin passing downward over the stomach walls. These waves, small at first, gradually become larger and larger until they finally involve the whole lower half of the organ, and the gastric musculature often passes into a condition of semi-tetanus. Then, quite suddenly, the contractions cease and an inactive interval of an hour or more ensues. After this period of quiescence the small waves begin again, and the entire process is repeated. Thus one period follows another as long as the stomach remains empty.

Gastric movements in both animals and man have been studied by means of the apparatus shown in figure 4 (Martin and Rogers, 1927). A balloon attached to the end of a tube is passed through the oesophagus into the stomach and inflated, and a manometer is fastened to the other end of the tube. The contractions of the stomach change the pressure on the balloon, so that some of the air is pushed up into the tube, and the level of the water in the manometer is changed. As the water rises and falls with the contraction waves, the movement is recorded by a floating pointer on a smoked drum. A record obtained by this method with similar apparatus is shown in figure 5. The record was taken in this laboratory on a human adult during a night of normal sleep. The portion presented,—that portion registered between 12.30 and 2.30, when the last meal had certainly been assimilated,—illustrates very clearly the cyclic nature of the movements of the empty stomach.

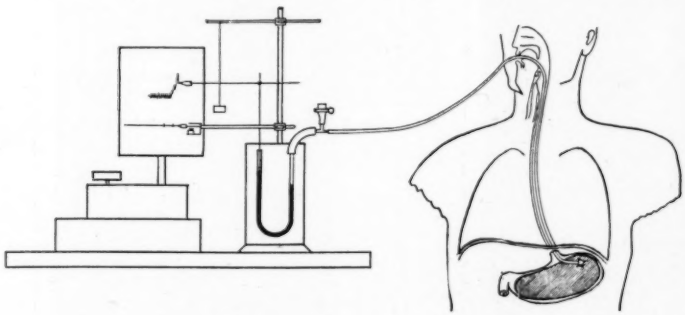

FIG. 4. DIAGRAM SHOWING THE METHOD OF RECORDING THE HUNGER CONTRACTIONS OF THE EMPTY STOMACH (Martin and Rogers, 1927)

According to the recent observations of Rogers and Martin (1926), the stomach takes the shape shown in figure 6 *A* at

the height of each of the single contractions near the end of the active period and that shown in figure 6 *B* when it is inactive and relaxed. With each of these large waves, then, we see that the lower part of the stomach contracts to such an extent that the lumen practically disappears, whereas the upper part may show a contraction wave near the middle.

Cannon and Washburn (1912) and Cannon (1915) have shown that with these

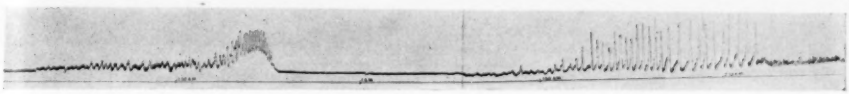

FIG. 5. RECORD OF STOMACH CONTRACTIONS OF A HUMAN ADULT TAKEN DURING AN UNINTERRUPTED SLEEP

large contractions the sensation of hunger arises, and from the work of Rogers and Martin we know that these "hunger" contractions are set up in the lower third

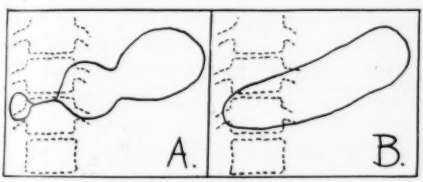

FIG. 6. *A.* SHAPE OF THE STOMACH AT THE HEIGHT OF A CONTRACTION WAVE. *B.* SHAPE OF THE RELAXED STOMACH

(Roentgenographic observations by Rogers and Martin, 1926.)

of the stomach. The hunger sensation is not produced until the end of the active period is nearly reached, when the waves have become very large, but even then it increases in intensity to some extent with the magnitude of the contraction, and it disappears entirely when the contractions cease. The inference, therefore, is quite logical that the two-hour periods of gross bodily activity in the rat are associated with periods of gastric movement and have to do with the hunger responses of the animal.

CORRELATION BETWEEN THE TWO-HOUR ACTIVITY RHYTHM AND THE HUNGER RESPONSE

In order to test this hypothesis we recorded simultaneously the bodily activity of the animal and the intervals at which it sought food and ate. This experiment was performed in the type of cage shown in figure 7. The larger compartment was simply the usual triangular

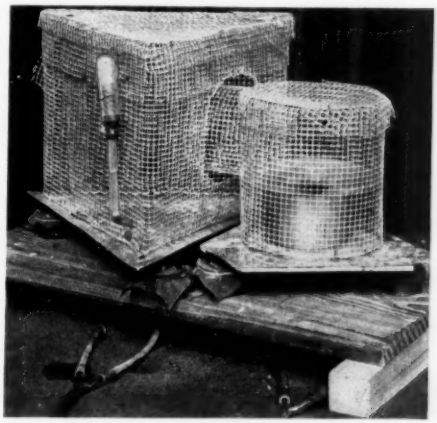

FIG. 7. PHOTOGRAPH OF COMBINED FOOD AND ACTIVITY CAGE

The two compartments are supported on separate sets of tambours so that the activity in each is recorded separately.

activity cage shown in figure 1; the smaller compartment contained a cup filled with a powdered food mixture (McCollum diet). The corners of each cage were supported on rubber tambours and so arranged that the activity in the two cages was recorded separately. In this way the curve in figure 8 was obtained,

where the activity in the large cage is registered on the first line, and that in the food-box on the second, with the time in hours below. It will be seen immediately that the animal always enters the feeding-cage and eats once during each approaches the food-box *except to eat*, and that the vibrations recorded in the activity cage for a short time after it leaves the food-box are produced almost entirely by an extensive cleansing performance which always follows feeding.

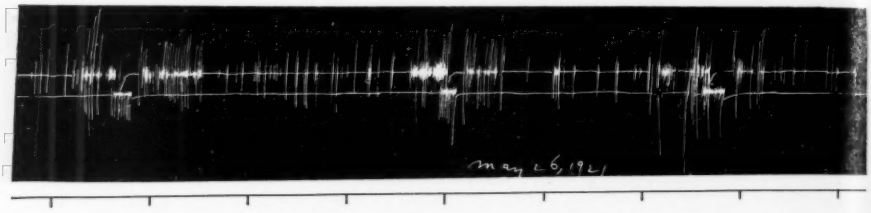

FIG. 8. RECORD SHOWING THE RELATION BETWEEN GROSS BODILY ACTIVITY AND FEEDING PERIODS

Activity in the large cage is given on the upper line, and entrances into the food-box on the lower. Time in hours is indicated below the record.

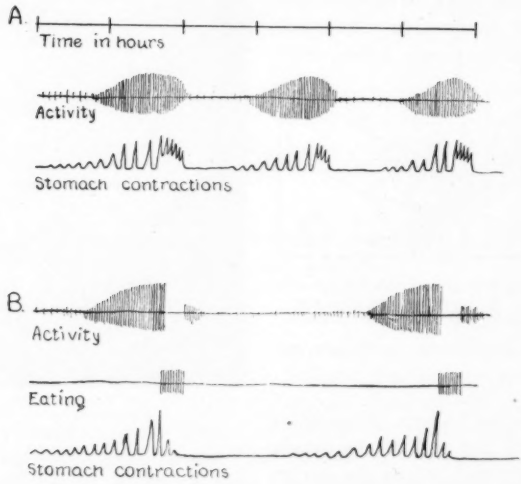

FIG. 9. SCHEMATIC REPRESENTATION OF THE RELATION BETWEEN PERIODS OF GROSS BODILY ACTIVITY AND STOMACH CONTRACTIONS

A. Simple activity cage without food. *B.* Double cage with food

activity period, that it enters usually near the end of the period and rarely at the beginning, and that it does not enter during a quiescent interval. Moreover, we have found through prolonged personal observation, that an adult animal rarely

In these experiments the activity periods, recurring invariably with the entrance into the food-box, are even more regular than they were in the earlier work when no food was available. With this greater regularity, the quiescent intervals are

much longer, so that the lapse between periods is three to four hours instead of one to two, as found in the activity cage with no food-box attached. The significance of the lengthened intervals will be discussed below.

We may now attempt to show in more detail how the gross bodily activity, the feeding habits, and the stomach contractions seem to be correlated. The simultaneous records of activity and feeding suggest that a close relationship must exist between the periods observed in the simple activity cage and the hunger "drive" of the animal. From the experimental data compiled above we know that the motility rhythm and the stomach contraction rhythm have three features in common: the frequency of both varies between one and two hours; the active phases of both begin at slight intensity and increase gradually, reaching a maximum near the end; and in both the active period ends abruptly and is followed by a quiescent interval. If we represent the two rhythms as in figure 9 *A*, drawing a diagrammatic activity record directly above a diagrammatic record of gastric movement, so that the active phases of the two coincide, we find that the small stomach contractions occur simultaneously with the beginning of the motility period, and that as the magnitude of the contractions increases the animal becomes more and more active. But how can we justify our representation in terms of the hunger response? It is very probable that as long as the animal experiences the hunger sensation which accompanies the stomach movements, it seeks for food, unsuccessfully, of course, in the single cage without a food-box. When the gastric contractions stop, however, the hunger disappears and the animal becomes quiet again.

On this basis one might expect that when food was available all the time, the rat would enter the food-box as soon as the contractions began. Actually, however, we know that it moves about in the main cage for some time before it approaches the food-box. How, then, can we explain this preliminary diffuse activity? Here again, as in figure 9 *A*, the relationship may be represented schematically. In figure 9 *B*, a record taken simultaneously from the activity cage and the food-box is shown in diagram on the first and second lines, and a stomach contraction record on the third. Thus we see that the small contractions give rise to the diffuse activity in the large cage. The animal seems at first simply to be annoyed and becomes more and more restless as the contractions grow larger, until the "main" contractions set in and the general discomfort becomes centralized in the hunger sensation. This stimulus dominates the behavior of the organism and it enters the food-box to eat. When its appetite has been satisfied, it passes into a period of quiescence which lasts until the stomach has become empty and the contractions have started up again. And since time is required for the contents of the stomach to be digested, the interval between contraction periods is three to four hours instead of one to two hours as observed in the earlier experiments.

We had hoped to establish this relationship in more detail in the rat by means of records taken simultaneously of stomach contractions and gross bodily activity, but all of our attempts to introduce balloons into the stomach of this animal were unsuccessful. It is very difficult to keep it from biting a hole in the tube in the first place. Furthermore, its throat is apparently too small to admit even the finest tube without a severe asphyxia resulting. Because of this failure, we turned our attention to other animals

from which Carlson and his associates had already obtained good records of stomach contractions.

Since the stomach tube can be introduced and fastened very easily in the bullfrog, we experimented on this animal, using the technique of Patterson (1915). The tube and bulb were pushed into the stomach through a small hole made in the skin beneath the throat, and the frog was placed in an activity cage enclosed in a box which could be almost completely darkened. Water from a faucet dripped through on the animal at all times in order to keep it in good condition. In this way

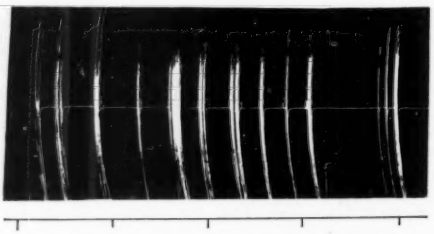

FIG. 10. RECORD SHOWING THE PERIODIC ACTIVITY OF A PIGEON, KEPT IN A LARGE CAGE WITH A PERCH

The bird spent most of its time on the perch, but at quite regular intervals it jumped down to the floor for a few minutes. This record shows the activity on the floor. Time is given in hours below the record.

we obtained stomach contractions which showed no periodicity at all. In one individual, in fact, both the frequency and the amplitude remained constant for eighteen days. The lack of periodicity partly defeated the purpose of the experiment, but not as much as the fact that the frogs remained perfectly still at all times, never making even the slightest movement.

The pigeon seemed more promising for our purposes, since we had previously found its activity to be definitely periodic. The intervals between the periods are somewhat shorter here than they are in the rat, but they are just as regular. The cage used in these experiments was cylindrical in shape, two feet in diameter and three feet high. The circular bottom, made of cardboard, and small enough to fit inside the wire wall without touching it at any point, was supported on tambours so that all movements of the pigeon were recorded on a smoked paper. A wooden rod pushed through the wire wall half-way up, pivoted on a nail at one end and supported on a tambour at the other, served as a perch from which activity could also be recorded. Figure 10, a record of the activity on the bottom of the cage when no food was available, shows that the bird left the perch about once every 20 minutes; and by attaching a recording food-box filled with corn, we found that every time it jumped down it invariably stopped to eat. Rogers (1916) has demonstrated a thirty-minute average rate for the active period of the crop of the pigeon, observing at the same time that it was most restless when its crop was contracting. We attempted, therefore, to record simultaneously the crop contractions and the activity in the larger cage, but the bird always managed to expel the tube no matter how carefully it had been inserted and fixed.

We sought our relationship next in experiments on the human infant. Wada (1922) found that in a child ten months old, during a continuous uninterrupted sleep lasting eight hours, the activity, as recorded by a tambour and spring placed beneath the crib, was definitely periodic, the interval between the periods averaging forty-five minutes. This seemed to offer us an excellent opportunity, especially since Carlson and Ginsburg (1915) had found that the stomach tube could be passed quite easily into infants. Our plan was to take simultaneous records of the stomach contractions and the activity

periods during sleep. In six babies used for these experiments we succeeded in passing the tube without too much difficulty, but then either the babies would not go to sleep, or else the tube was completely blocked by strong spasms of the cardiac results. The students swallowed the stomach tube at ten o'clock in the evening, just before retiring, and simultaneous records were taken throughout the night of the stomach contractions and bodily movements. Besides diffuse ac-

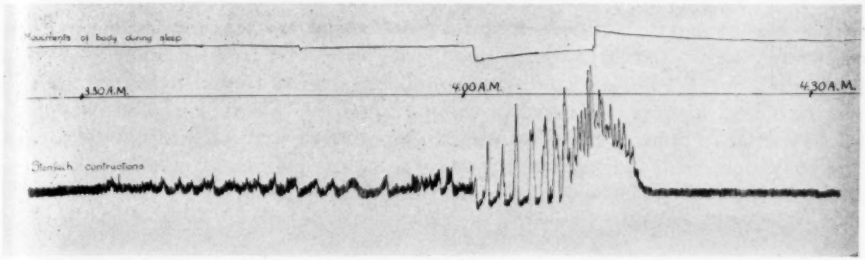

FIG. 11. SIMULTANEOUS RECORD OF GROSS BODILY MOVEMENT AND STOMACH CONTRACTIONS OF A HUMAN ADULT TAKEN DURING DEEP SLEEP

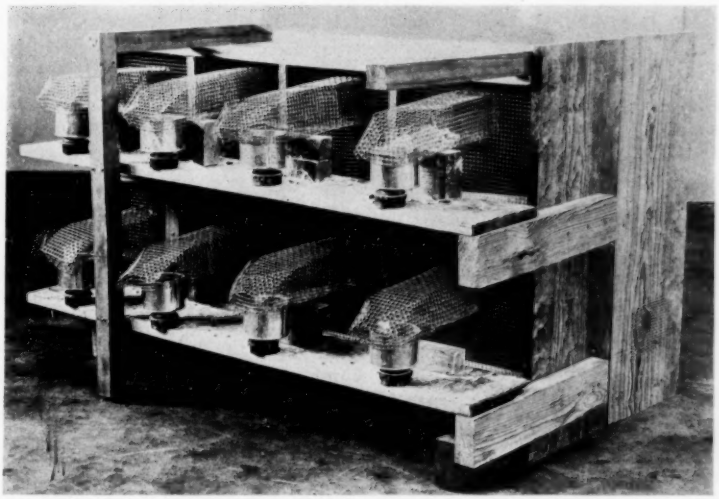

FIG. 12. CAGES USED FOR STUDYING FOOD-HABITS

sphincter. After many unsuccessful attempts this method of attack had to be abandoned.

Meanwhile, Wada, taking records on medical students while they slept, succeeded in obtaining some very conclusive tivities such as turning over, smaller movements were recorded whenever possible. Adult activity during sleep, just as infant activity, proved to be periodic, but the interval between the periods is much longer, varying between two and three

hours. The stomach contractions, of course, are also rhythmical, much more so than they are during the waking state. And the periods of these two phenomena coincide very well; when the stomach is quiescent the gross bodily activity is reduced to a minimum, but during the contraction periods frequent movements occur, the largest coinciding with the "main" hunger contractions. The record in figure 11 illustrating this fact is similar to those obtained by Wada. The body movements indicated on the top line in this figure were recorded by means of a tambour and spring attached from beneath to the spring of the bed. Since only large movements such as turning over are registered in this way, it can be seen that just before the "main" hunger contractions set in, the subject became very active, and again almost simultaneously with the largest contraction wave there was an even greater amount of activity.

The results of most of our supplementary experiments, therefore, while not conclusive, would seem to uphold our theory that the two-hour activity rhythm in the rat is dependent on gastric function.

FEEDING HABITS OF THE RAT

Starting from our observations on the relation between activity and the feeding periods of the rat, we decided to extend our investigation to a study of its food habits, with special reference to their regularity. For this purpose cages shown in figure 12 were constructed. They consisted of individual compartments large enough for the animals to take plenty of exercise, with a small tunnel on one side at the top leading to the food-box. This tunnel was built in an inconvenient position in order to discourage the rat as much as possible from entering it except when driven by hunger. The food-cup was placed at the end of the tunnel under the wire cloth floor, and a hole was made in the floor just large enough for the rat to insert its head. Whenever it reached in for food, the balance of the cup on a large tambour was disturbed and a mark was made on a smoked drum.

FIG. 13. RECORD SHOWING THE FEEDING PERIODS OF AN ADULT RAT
Time is registered at half-hour intervals

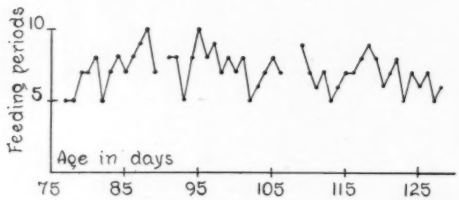

FIG. 14. GRAPH SHOWING THE REGULARITY OF THE FEEDING PERIODS OF AN ADULT RAT FROM DAY TO DAY

The number of periods per day is given on the ordinates and the age of the animal in days on the abscissae.

The records obtained in these cages bring out clearly the great constancy of the feeding habits of the rat. The record in figure 13, taken on an adult animal from 8 p.m. to 8 a.m., shows that the feeding period recurred about once every three hours throughout the day, and when the experiments were extended over a longer time, it was found that the rhythm persisted very constantly from day to day (See fig. 14). Similar experiments on

other animals confirmed these results. A rat may eat seven times a day or it may eat eight or ten times, but in any case it maintains a constant average from one day to the next. The degree of variability of the feeding response is shown very clearly by the curve in figure 15, compiled from records taken on four animals for twenty successive days. The abscissae represent the length of the intervals recorded between feedings, and the ordinates indicate the number of times each interval was recorded from any one of the four individuals. The curve is evenly balanced with a mode of two hundred and fifty minutes, or approximately four hours. The few longer intervals, we believe, may be identified entirely with periods during which the rat, like the human being, slept in spite of the stomach contractions.

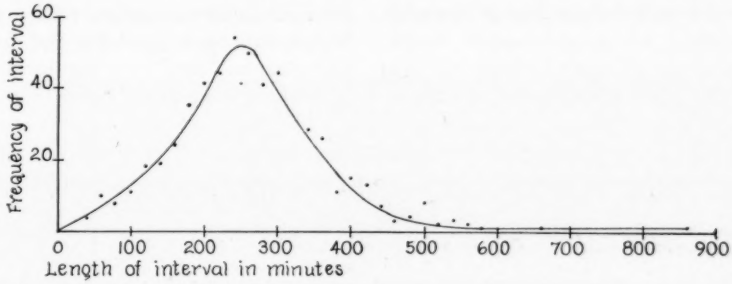

FIG. 15. FREQUENCY CURVE OF INTERVALS OF VARIOUS LENGTHS BETWEEN FEEDING PERIODS IN FOUR ADULT MALE RATS FOR TWENTY DAYS

From the above experiments it seems fairly well established, then, that the hunger contractions stimulate the organism to activity, but what the details of the mechanism are we are not prepared to discuss. We do believe, however, that somehow, with each new hunger contraction period, impulses are sent up the afferent nerves from the stomach to the brain and out to the striped muscles, to release the energy stored up there.

GENESIS AND DEVELOPMENT OF THE FEEDING HABITS

But how does the activity produced in this way become associated finally with the eating process? We cannot assume that the new-born animal seeks food

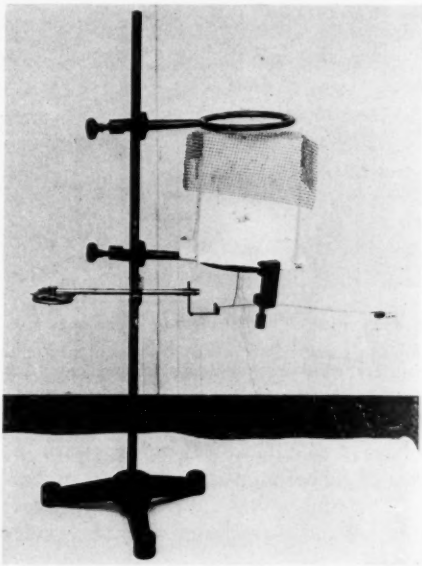

FIG. 16. PHOTOGRAPHS OF CAGES USED IN RECORDING ACTIVITY OF NEW-BORN RATS

when the contractions begin. Indeed it would seem more probable that the relationship is built up by the usual trial and error method. In order to solve this problem one must learn more about the activity of the very young animal. Does it show the periodic motility of the adult individual?

The activity of the new-born rat was recorded from the cages shown in figure 16. The bottom of the cage consisted of a wooden frame 6 inches square with a sheet of rubber dam stretched taut across it. The rubber was covered with pieces of flannel and the sides of the cage, made of paper, were pasted on the wooden frame. Every movement of the animal in the cage was transmitted through the rubber membrane to a lever which recorded on a smoked paper drum. The young rats were left in the cages for twelve hours at a time, and then returned to their mothers for twelve hours.

Records obtained in this way showed that the motility of the rat immediately after birth is continuous rather than periodic (See fig. 17). For the first ten days it remains constant; then a rhythm begins to appear, and by the sixteenth day clear-cut and very regular intervals are present. This result is consistent with the fact that the new-born of some animal species show stomach contractions with almost no indication of periodicity (Patterson, 1914). On the basis of this knowledge, then, we may picture how the diffuse activity of the new-born rat resolves itself into a search for food.

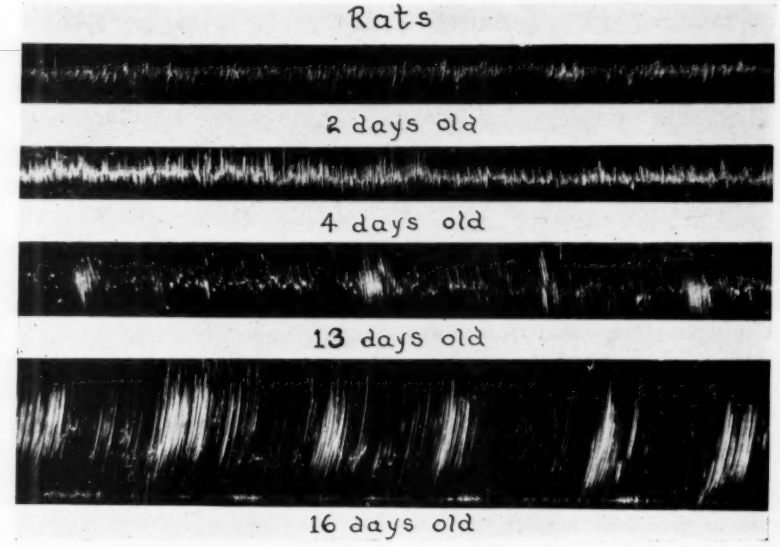

FIG. 17. RECORD OF THE ACTIVITY OF A NEW-BORN RAT TWO, FOUR, THIRTEEN, AND SIXTEEN DAYS AFTER BIRTH

Up to the tenth day the activity is continuous, then it gradually breaks into periods, which, by the seventeenth day, stand out very clearly in the records.

In its almost continuous motility, the very young animal sucks at everything with which its mouth comes into contact,—the feet and legs of its litter

mates, the straw of the nest, hair on its mother's body, and, eventually, the mother's teats. When it sucks at anything other than the teats, nothing results; the stomach contractions persist and the activity continues as before. When it sucks at the teats, on the other hand, an entirely different situation arises; milk fills the stomach, the contractions cease, and the animal grows quiet. Then as the stomach becomes empty again, the process will be repeated. The animal may happen upon the teats at the very beginning, or it may reach them after a prolonged active interval. In either event, the excursion always ends with the feeding process. The young doubtless frequently find the teats through the intervention of the mother, but largely by the trial and error method there is gradually established, on a conditioned reflex basis, an association between discomfort due to stomach contractions, feeding, and subsequent relief. In the adult rat, the preliminary restlessness which occurs during the time of small contractions is diverted at once into specific food seeking activities as soon as the main contractions begin.

FIG. 18. ACTIVITY RECORDS OF NEW-BORN ANIMALS
A, rabbit and kitten. *B*, chicken. Time in hours below the record

It is interesting in this connection that the new-born guinea pig, rabbit, kitten, and chick, unlike the rat, show periodic activity at birth (See fig. 18 *A* and *B*). But how may this fact be brought into relation with the view developed above?

It is important to note that while the rat is still in a comparatively embryonic condition at birth, these other animals are all fairly well developed and coördinated. The rat, for several days after birth, progresses much as a worm does, crawling and wriggling its way about; the new-born guinea pig, on the other hand, actually walks almost at once. In keeping with their periodic bodily activity, the more highly developed individuals probably show periodic stomach contractions at birth. We have as yet done no experiments to test this theory, but we hope soon to observe in detail the feeding habits of these animals to determine how the habits differ from those of the rat with regard to their genesis and development.

FURTHER OBSERVATIONS ON THE PERIODIC NATURE OF SPONTANEOUS ACTIVITY. FOUR-DAY ACTIVITY RHYTHM IN THE FEMALE

So much for the three to four-hour activity rhythm apparent in records taken during twelve to twenty-four hour periods. Our observations must now be extended over days and weeks instead of hours. The small triangular cages are impractical for this purpose because of the length of time required to count the individual marks on the smoked drum record. Activity for long periods can be measured more simply and much more accurately in the type of cage shown in figure 19, which consists of a small living

FIG. 19. APPARATUS USED FOR MEASURING SPONTANEOUS RUNNING ACTIVITY

The living compartment with the food cup and water bottle, and the cyclometer and lever, can be seen on one side of the partition, and the revolving drum on the other side. (Richter and Wang, 1926.)

compartment just large enough to accommodate a food-cup and an adult animal, and a revolving drum to which the animal has free access at all times. By means of a cyclometer connected with the axle of the drum by an excentric lever, all revolutions, clockwise and counter clockwise, are recorded. A detailed description of the complete apparatus and method employed is given elsewhere (Richter and Wang, 1926; Richter, 1926; Wang, 1927).

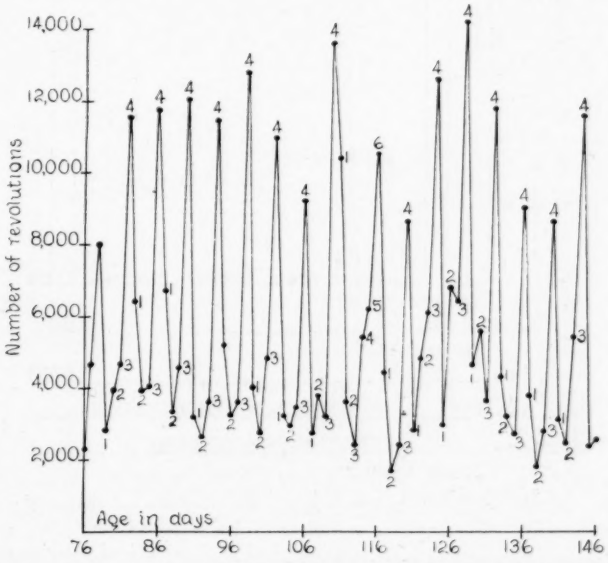

FIG. 20. RUNNING RECORD OF A NORMAL FEMALE SHOWING THE FOUR-DAY CYCLE

The rat, like many other small rodents, seems to enjoy running and spends much of its time in the drum. Although the daily activity averages between five and ten miles for most of the animals, as many as twenty-seven miles have been recorded for one individual in twenty-four hours.

Here again, casual observation of the running activity discloses nothing of its origin. Continuous records over long periods of time, however, reveal a fact far more striking than the tri-hourly rhythm described above. In the female rat the activity falls into a regular four-day cycle, most females running eight to ten miles every fourth day and but a fraction of a mile on the three days intervening. In the record in figure 20, in which activity measured in the number of revolutions is indicated on the ordinates, and the days of the experiment on the abscissae, the regular four-day peak is very evident. Since this rhythm, which was described independently by Wang (1923) and Slonaker (1924), occurs in an environment free from any cyclic disturbance, it, too, must have its origin within the organism. But what organ functions in the rat at a four-day rhythm?

FOUR-DAY ACTIVITY RHYTHM AND THE OVULATION CYCLE

Observations of the ovulation cycle of the rat made by Long and Evans (1922) answer this question at once. These

workers have shown, by the methods of Stockard and Papanicolaou (1917), that the length of the oestrous cycle in the rat is four days, with individual variations above and below this average. As is well-known, this was determined by histological studies of cast-off cells scraped with a small spatula from the vaginal mucosa. During the dioestrum nucleated epithelial cells and leucocytes are present, whereas during the periods of oestrus and ovulation only cornified cells appear.

Wang and Slonaker have been able to show by means of simultaneous smear and activity records, that the peak of running activity every fourth day just precedes ovulation. This is undoubtedly one of the most interesting correlations that have been made in animal behavior.

The question arises then, as to the relation between the running activity and the sex "drive" of the animal. Wang has found that females will mate for a short time just before and just after the peak of running activity is reached, while at all other times they are completely indifferent or even averse to the male. The exact relationship between running activity, vaginal smears, and sex activity, as worked out by Wang, is shown in figure 21. Records taken every six hours on all three phenomena showed that the great burst in running activity recorded on the day of oestrus is confined almost entirely to the six-hour interval which immediately precedes the appearance of cornified cells in the vaginal smear.

Obviously, therefore, the spontaneous activity is dependent on ovarian function. The degree of dependence can be demonstrated directly by numerous experiments performed on animals in which the ovaries

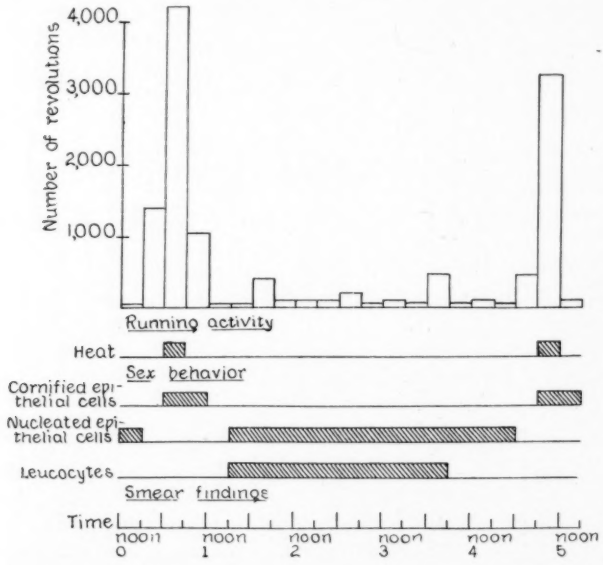

FIG. 21. EXACT TEMPORAL RELATIONSHIP BETWEEN RUNNING ACTIVITY AND THE OVULATION CYCLE, ESTABLISHED BY MEANS OF SIX HOUR RECORDS

(After Wang, 1923)

were not functioning. Pre-pubescence, senility, pregnancy, pseudo-pregnancy, lactation, and castration all show a clear-cut effect in the activity readings. In figure 22, a typical normal record is presented to show the low running level before puberty and the sudden pubescent burst.

Pregnancy causes a 60 to 95 per cent decrease in activity which lasts through the entire gestation and lactation period (Slonaker, 1925; Wang, 1923. See fig. 23). Pseudo-pregnancy, produced when the tip of the uterus is stimulated with a glass rod introduced through the vagina, results in an immediate decrease which persists for fifteen days (Wang, 1923. See fig. 24), and sterile copulation performed by a vasectomized male has the same effect (Slonaker, 1925).

Similar results were obtained in a series of experiments in which a normal female had constant access to a cage containing a vasectomized male. In these experiments a sex-box attached to the usual living-cage connected with the revolving drum, was so arranged that the female could pass freely back and forth to visit the male, but the male could not get into the living cage and revolving drum. This separation was achieved quite simply by means of a board partition with a hole just large enough to admit the female, but too small for the male. A typical record obtained in this way is shown in figure 25. In order that we might differentiate running activity changes caused by the extra compartment from those caused by the presence of the male, we attached the sex-box a week before the male was introduced. The record shows that the mere addition of the sex cage produced no

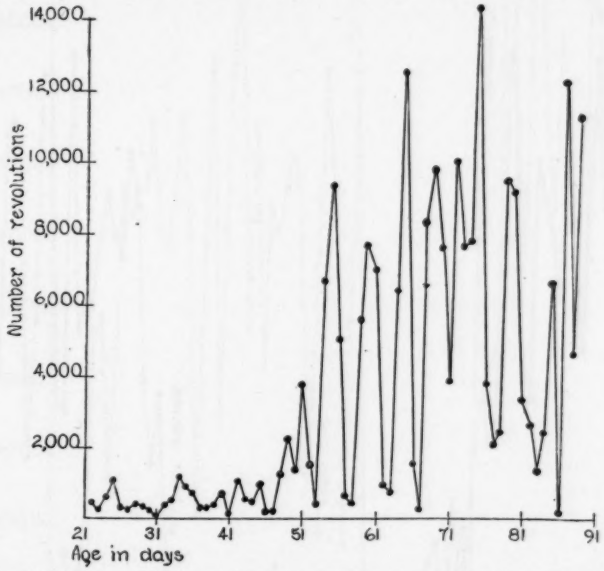

FIG. 22. RECORD SHOWING THE BURST OF ACTIVITY AND APPEARANCE OF THE FOUR-DAY CYCLE AT THE TIME OF PUBERTY

(After Wang)

effect. When the male was placed in it, however, there was an immediate and prolonged decrease in activity which persisted for eight to ten days after he was removed again.

Figure 26 shows the effect of complete removal of the ovaries: the activity drops (60 to 95 per cent) to a flat, low level and the four-day cycle disappears completely. When an animal is spayed before puberty its activity always remains low and non-rhythmical (Wang, 1923; Slonaker, 1924).

Finally the dependence of the running activity on the ovaries may be demonstrated most strikingly by the effects of ovarian implantation in spayed animals. Whenever the grafts "take," the activity begins to increase almost immediately, and it grows gradually higher until the normal running level of the female is reached. Then, if the grafted ovary is removed, the activity drops about 60 to 95 per cent, just as it does in the normal female after spaying.

These experiments show definitely that the high running level is dependent upon some substance secreted by the ovaries into the blood stream. The question now

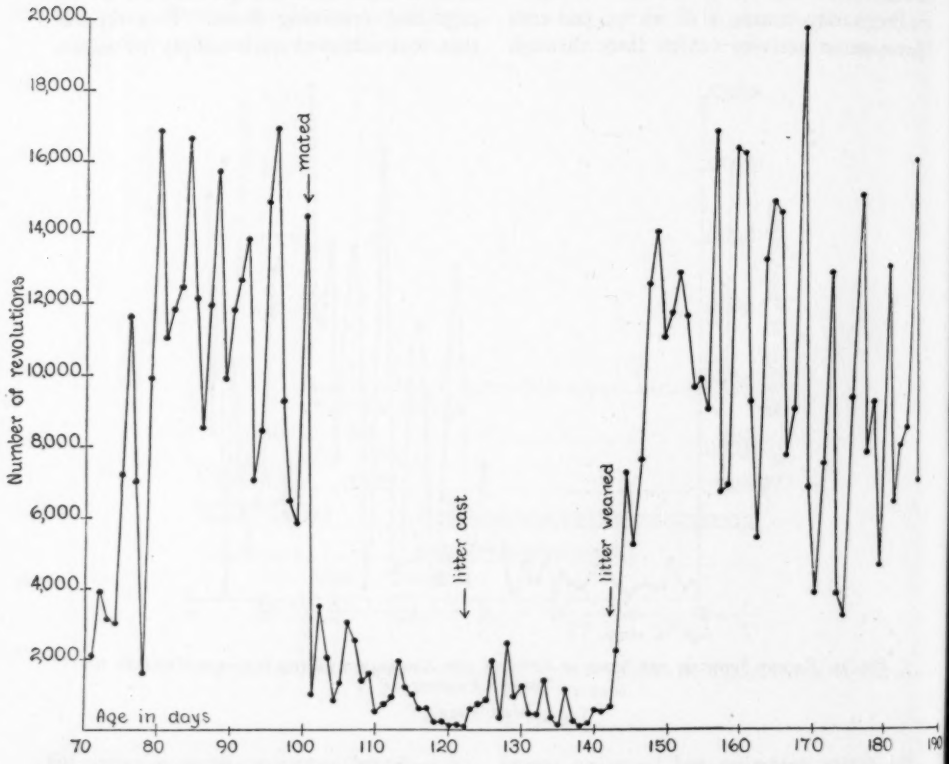

FIG. 23. RECORD SHOWING THE EFFECT OF PREGNANCY AND LACTATION ON SPONTANEOUS ACTIVITY

The four-day cycle is absent during pregnancy and lactation, appearing again a short time after the litter is weaned. (After Wang.)

arises as to what part of the ovaries produces this substance. Bugbee and Simond (1926) have thrown some light on this problem by experiments in which the extract from pigs' follicles was injected into spayed rats. Such a procedure produces the same effect that successful implantation of an ovary would have produced,—the activity shows a marked increase from the low spayed level to the level of normal animals and the genital tract resumes its normal condition.

Wang also has obtained these results by the injection of follicular extracts (Unpublished results. See fig. 27). He found that the smear changes are usually detected several days before the activity changes become well defined, and in many instances the activity and smear changes occur independently of each other. Ac-

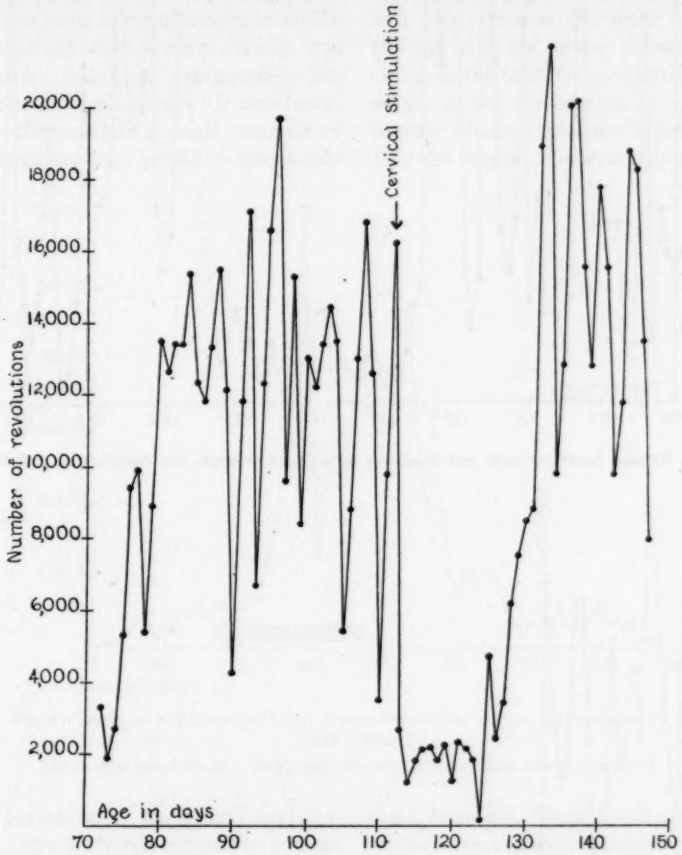

FIG. 24. EFFECT OF PSEUDO-PREGNANCY ON ACTIVITY
(After Wang)

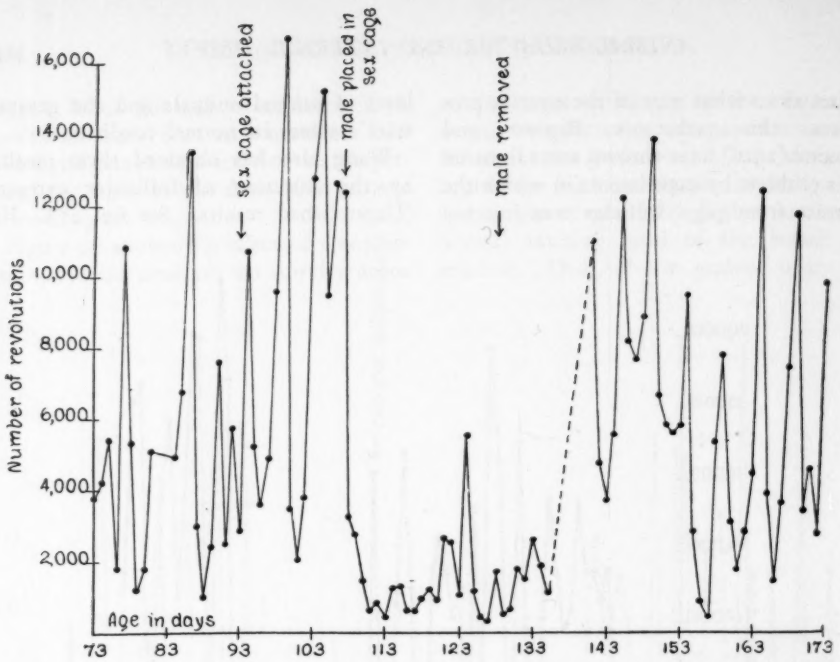

FIG. 25. RECORD SHOWING HOW THE PRESENCE OF A MALE AFFECTS THE ACTIVITY OF THE FEMALE

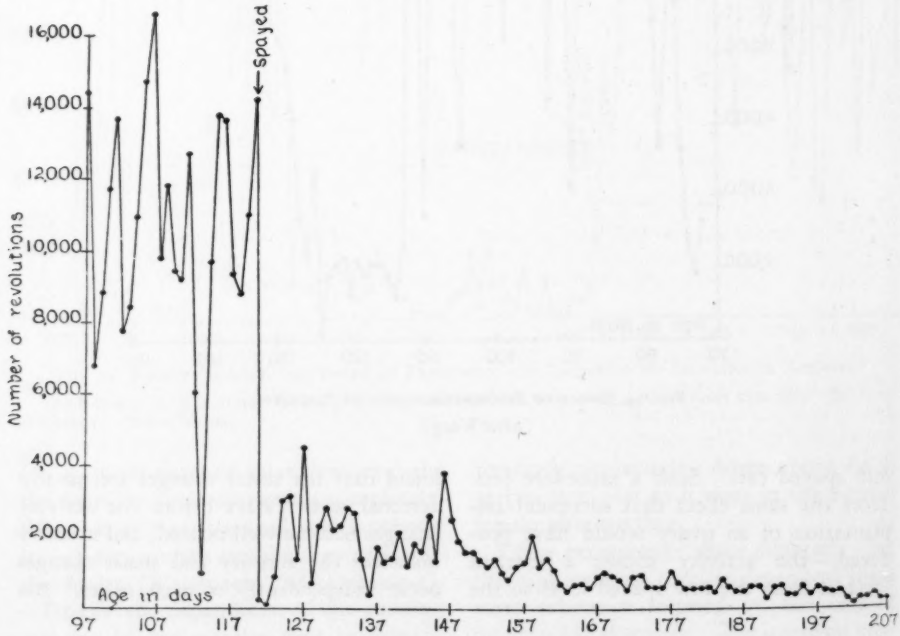

FIG. 26. RECORD SHOWING THE EFFECT OF THE COMPLETE REMOVAL OF BOTH OVARIES

cordingly he has concluded that there may be in the ovarian secretion one specific substance for furthering the growth and development of the genital tract and another for the production of activity. And on the basis of experiments in which he traumatized the ovaries (Wang and Guttmacher, 1927), this suggestion becomes even more plausible. It was found quite by chance that a small remnant of ovary left in the body produces very striking changes in both smear and activity findings. The activity, except for a drop of short duration immediately following the operation, usually regains its original level, but the four-day cycle is entirely absent. Coincident with the high irrhythmic activity level, the vaginal smears usually show cornified cells, the indication of oestrum in the normal animal. In some individuals, however, the other types of cells, as well as cornified cells, appear and disappear with very little relation to the changes in activity.

The question as to how and where the secretion acts to produce the activity has not yet been answered. We thought at first that, just as the three to four-hour rhythm was set up by stomach contractions, so the four-day cycle might have its origin in the contraction of some similar hollow viscus in the sex-apparatus, probably the uterus. Contrary to our expectations, however, Wang found that removal of the uterus affects neither the level of activity nor the four-day cycle (fig. 28), and Hoskins (1925, II) has recently confirmed these observations. The secretion, then, must take effect in some part of the central nervous system, either by simply increasing the irritability of the centers in the brain and spinal cord, or by actually stimulating those centers. Although definite evidence is lacking at present, we

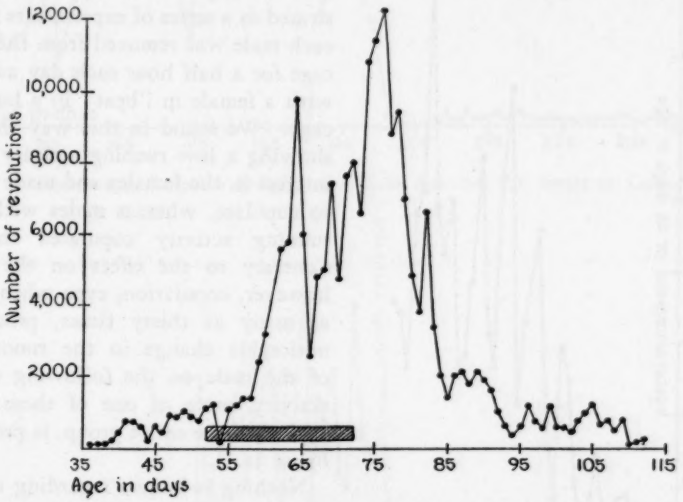

FIG. 27. RECORD SHOWING THE EFFECT OF DAILY INJECTIONS OF FOLLICIN ON THE RUNNING ACTIVITY OF A SPAYED FEMALE

The shaded area indicates the period over which the extract was administered

are inclined to hold to the latter possibility.

SPONTANEOUS RUNNING ACTIVITY OF THE MALE

In the male the spontaneous running activity does not show the four-day cycle of the female, and the general average is somewhat lower. However, it is dependent on the sex glands, for when the animal is castrated the activity drops about 60 per cent to the low level of the spayed female (fig. 29). Hoskins (1925, IV) was able to demonstrate no change in activity when testes were transplanted to the castrate, but we have found that the activity immediately increases to the normal running level (Richter and Wislocki, 1927). And transplantation of ovaries brings about an even greater increase (Wang, Richter, and Guttmacher, 1925). The activity then reaches the high level of the female, and, what is more interesting, it also shows the four-day rhythm (See fig. 30). When the grafts are removed the castrate effects appear again.

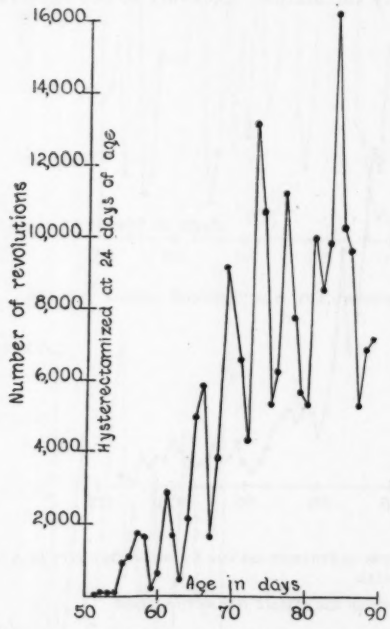

FIG. 28. RECORD SHOWING THAT REMOVAL OF THE UTERUS AFFECTS NEITHER THE LEVEL OF THE RUNNING ACTIVITY NOR THE APPEARANCE OF THE CYCLE

That the relation of running activity to the sex "drive" is not so clear-cut in the male as it is in the female, is demonstrated in a series of experiments in which each male was removed from the running cage for a half hour each day and placed with a female in "heat" in a large stock cage. We found in this way that males showing a low running activity took no interest in the females and made no effort to copulate, whereas males with a high running activity copulated frequently. Contrary to the effect on the females, however, copulation, even when repeated as many as thirty times, produced no noticeable change in the running level of the male on the following day. An activity curve of one of these animals, typical of the entire group, is presented in figure 31.

Nothing is known regarding the mechanism involved in the production of the activity of the male. That the removal of the seminal vesicles produced a no more noticeable effect than did the removal of the uterus in the female is shown in figure 32. We are trying to discover on what part of the testes the activity is dependent by a method similar to that used by Stockard and Papanicolaou in the female. We have been extirpating the testes in some animals at a peak of activity and in others at a depression with the expectation that detailed histological studies of these organs may disclose what parts are responsible for the fluctua-

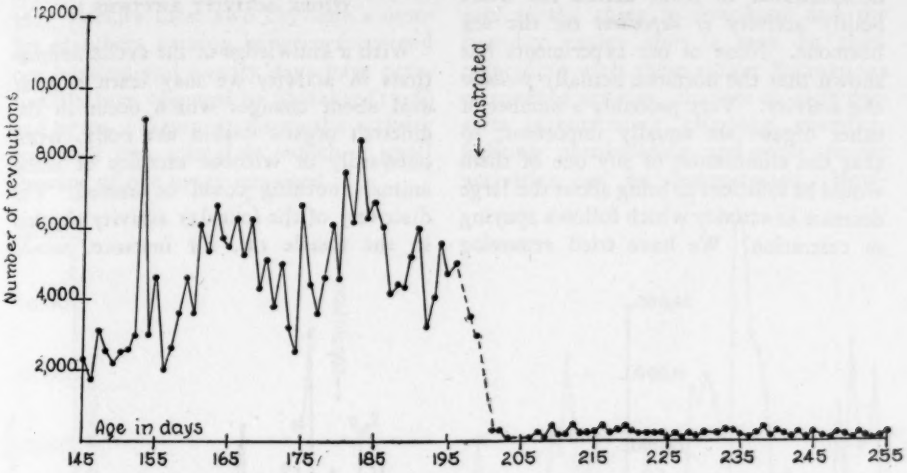

FIG. 29. SPONTANEOUS RUNNING ACTIVITY OF A MALE, SHOWING THE EFFECT OF CASTRATION

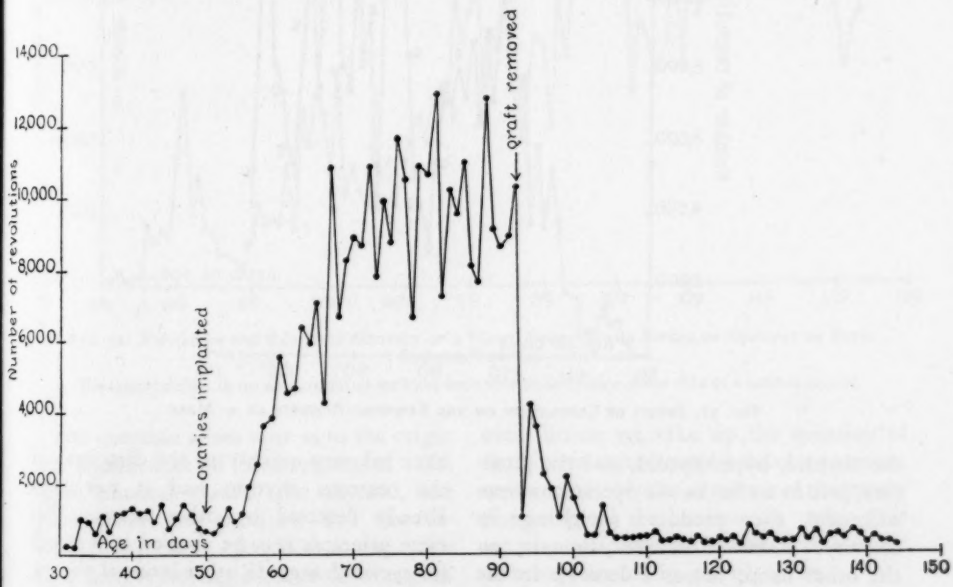

FIG. 30. RECORD SHOWING THE EFFECT OF IMPLANTATION OF OVARIES INTO A CASTRATED MALE

tions in activity. Although we have obtained no conclusive data the approach is promising.

It must be borne in mind before we pass on to a discussion of other rhythms that the work reported above has simply

demonstrated to what extent the overt bodily activity *is dependent* on the sex hormone. None of our experiments has shown that the hormone actually *produces* the activity. Very probably a number of other organs are equally important, so that the elimination of any one of them would be sufficient to bring about the large decrease in activity which follows spaying or castration. We have tried removing the thyroid, hyperthyroid, and the pituitary, but in so far as our operations were successful, they produced no change in activity. Removal of the adrenals, on the other hand, causes a decrease in the running average, although the sex cycle still remains (See fig. 33). It can be seen, then, that we still do not have complete knowledge of the mechanism which determines the composite picture of the spontaneous activity.

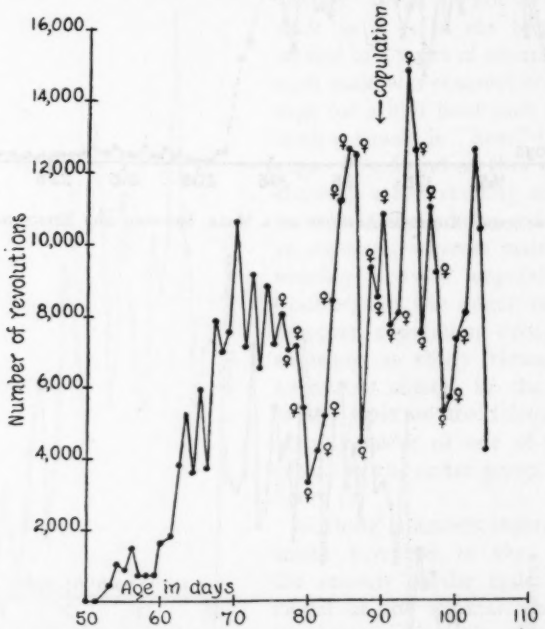

FIG. 31. EFFECT OF COPULATION ON THE RUNNING ACTIVITY OF A MALE

OTHER ACTIVITY RHYTHMS

With a knowledge of the cyclic fluctuations in activity we may learn a great deal about changes which occur in the different organs within the body, when outwardly or without sacrifice of many animals nothing could be learned. The discovery of the four-day activity rhythm in the female rat, for instance, would have led very quickly to the discovery of the oestrous rhythm had it not been already detected by other means. This same principle may be applied in a search for cyclic changes in other internal organs, since we have found periods of activity longer than four days in both males and females after the sex organs have been removed. There are at least two other fairly well-defined rhythms, one of from seven to ten days (fig. 34), and one of

from sixteen to thirty days (figs. 35 and 36). Besides these two rhythms a number of others varying between forty and one hundred and twenty days have occasionally been observed by Slonaker (1926) and by us. Figure 37 shows the activity record of one animal in which a small remnant of one ovary remained.

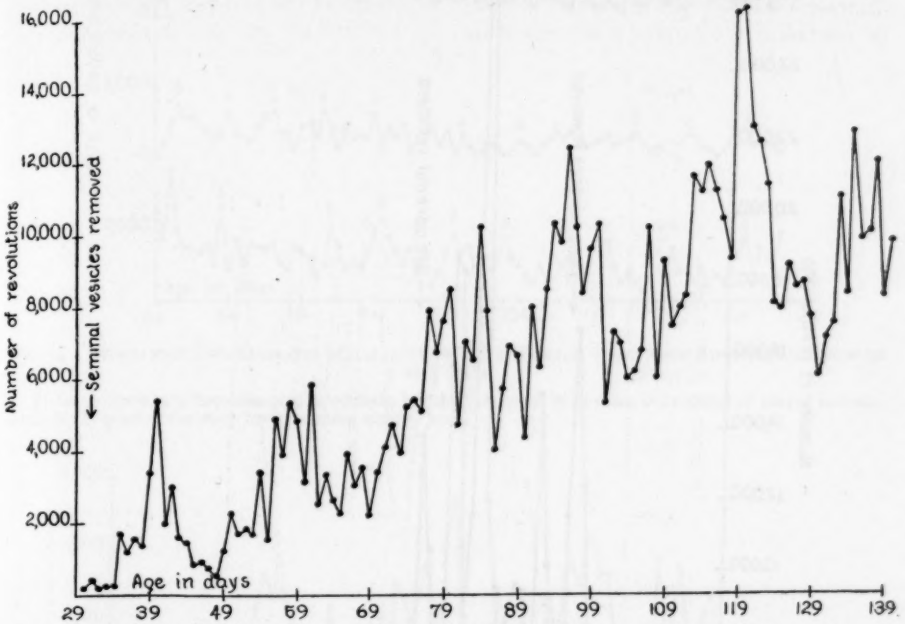

FIG. 32. RECORD OF THE RUNNING ACTIVITY OF A MALE, SHOWING THE EFFECT OF REMOVAL OF BOTH SEMINAL VESICLES

The record differs in no way, so far as we have been able to determine, from that of a normal animal

The question arises now as to the origin and significance of these rhythms. The other internal glands, the thyroid, the parathyroid, the pituitary and the adrenals, suggest a possible source. We have been removing each of these organs at various phases of activity but we have been unable as yet to make a study of the histological sections.

So much for the origin of these rhythms. What is their significance? Are they associated with some specific performance just as the three to four-hour and the four-day cycles are? It may be that, coinciding with these slower fluctuations of running activity, changes in such pursuits as burrowing, climbing, gnawing, fighting, nest-building, and other specific activities can be demonstrated. However, before we take up the question of these more complicated behavior patterns, we must consider briefly some of the purely physiological mechanisms in order that we may comprehend the complete activity picture presented by the organism.

OVERT RESPONSES OF A PURELY PHYSIOLOGICAL NATURE

For this reason we have studied drinking, urination, and defecation, to deter-

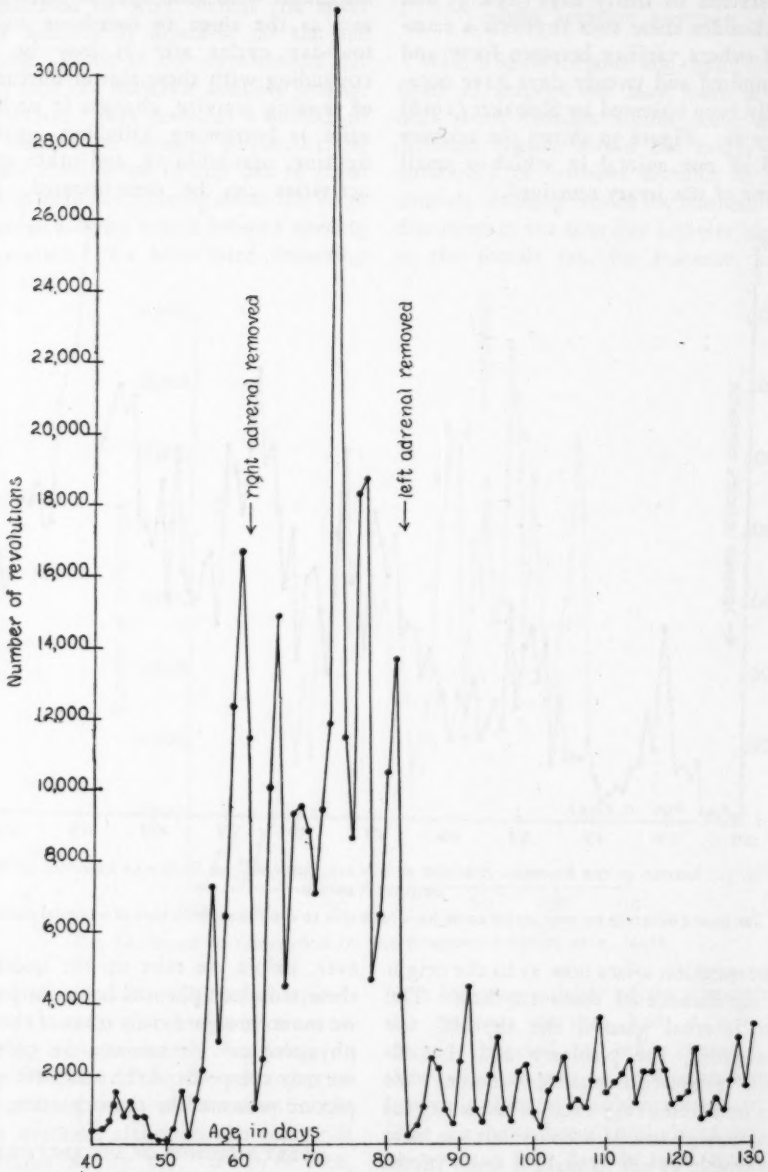

FIG. 33. RECORD SHOWING THE EFFECT OF THE REMOVAL OF BOTH ADRENALS

mine whether these functions, too, are periodic. Records of the time interval at which these three responses occur show that they are all rhythmical.

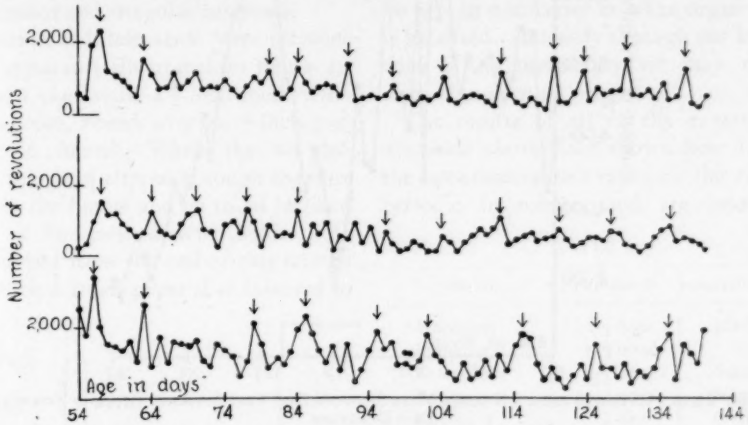

FIG. 34. ECORDS FROM TWO CASTRATED MALES AND ONE SPAYED FEMALE, WHICH SHOW RHYTHMS VARYING FROM 5 TO 8 DAYS

These rhythms have been observed in normals, but they are found most often in castrated or spayed animals probably because of the much lower running activity level.

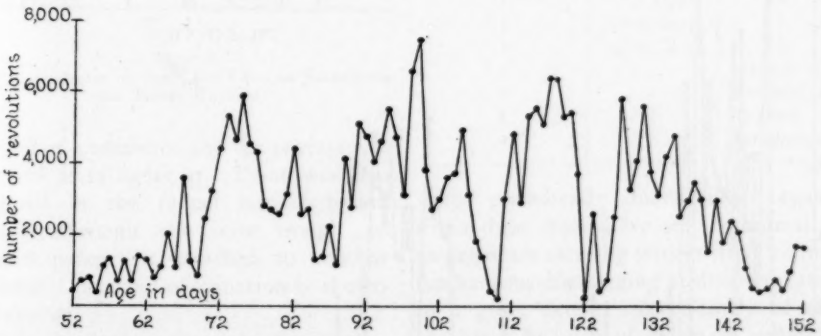

FIG. 35. RECORD OF A NORMAL MALE SHOWING A 16 TO 20 DAY CYCLIC CHANGE IN THE RUNNING ACTIVITY LEVEL

The cycles are much more irregular than the four-day cycle, but they are clearly present nevertheless.

Thirst was studied by means of the cages shown in figure 38. A recess large enough for the animal to enter and drink, but too small for it to lie down or turn around, was built on one side of the cage and an inverted watering tube was placed at the end away from the cage. The bottom of this recess was made of a piece of aluminum pivoted at one end and supported on a tambour at the other, so that whenever the animal entered to drink a mark was recorded on a smoked drum. The records, as may be seen in figure 39, show that the rat drinks about ten times

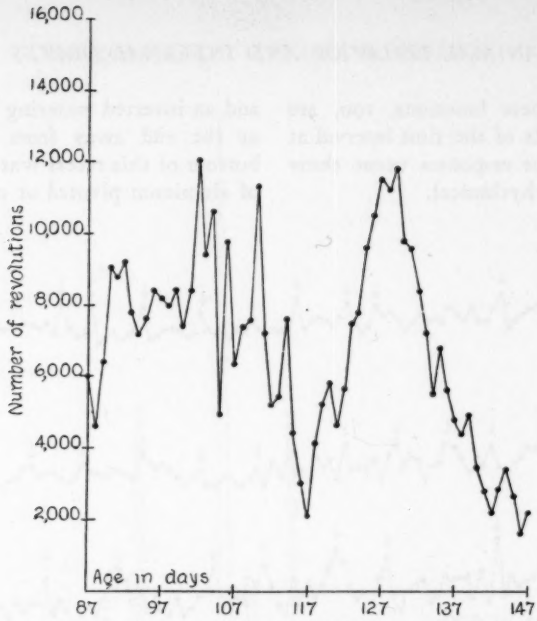

FIG. 36. RECORD OBTAINED FROM A NORMAL MALE SHOWING ONE VERY STRIKING CYCLE OF TWENTY-NINE DAYS DURATION

The activity mounts steadily for twelve days, then decreases again equally steadily for the next seventeen days. Such regular cycles often appear in the midst of an otherwise very irregular record.

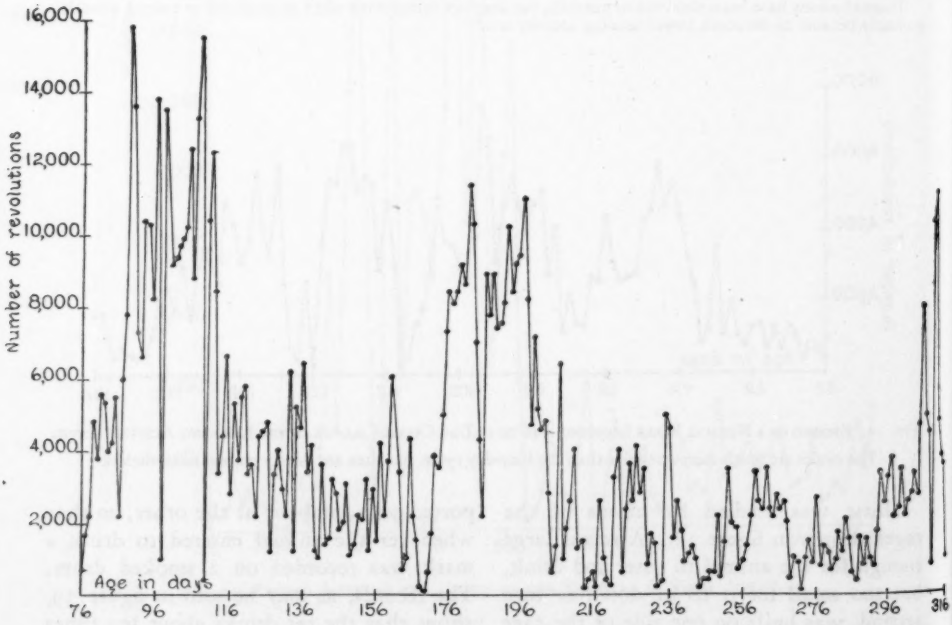

FIG. 37. GRAPH SHOWING CYCLES OF MUCH LARGER DURATION,—90 TO 120 DAYS

This record was obtained from a female with one ovary completely removed and the other partially cut away. The animal did not show the low activity of the spayed animal. On the contrary it showed cyclic fluctuations, during which it reached a level nearly as high as that present before the ovary was traumatized.

a day at intervals of two and a quarter hours. The periodicity of the thirst response is quite as remarkable as that of the hunger response, in view of the current conception that the rats eat and drink at very frequent and irregular intervals.

Urination and defecation were recorded in the apparatus illustrated in figure 40. The small cage with a ½-inch mesh wire-cloth bottom, rested over an 8-inch paraffined tin funnel. When the rat defecated, the feces slipped through the wire floor into the funnel and on to an inclined trough of fine-meshed wire below. As they dropped from the end of this trough they struck a small paper disc fastened to

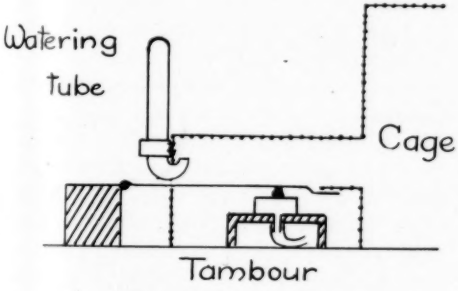

FIG. 38. DIAGRAM OF THE CAGE USED IN RECORDING THE THIRST RHYTHM

the end of a tambour, and the process was recorded as in figure 41. Urine was also collected in the funnel but it passed directly through the wire trough to another paper disc attached to another tambour. A record of urination is shown in figure 42.

From simultaneous records of urination and defecation obtained by this method, it was found that although these two functions are very regular, they are quite independent. Urination occurs approximately every two hours; defecation, every five hours, but the group of animals studied up to the present time is not sufficiently large to permit accurate statements of the time interval, nor can we show how these rhythms vary with age and sex.

These phenomena must reveal the periodicity of the bladder and rectum, but so far we do not know in what organ thirst is localized. Possibly through our knowledge of its periodicity we may obtain some clue as to its origin.

The results of all of the experiments discussed above have shown how largely the spontaneous activities of the rat are periodic in nature, and are associated with periodically functioning organs. From these results, we see the animal as an organism carrying within itself various mechanisms discharging at different rates, to a great extent independently of one another. By way of summary we have listed in Table I the different activities according to their periodicity and the organ with which they are associated.

TABLE I

ACTIVITY	PERIODICITY	ASSOCIATED ORGAN
Urination	2–3 hour	Bladder
Drinking	2–3 hour	?
Defecation	3–5 hour	Rectum
Eating	3–4 hour	Stomach
Mating ♀	4 day	Ovaries
Nest-building	?	?
Gnawing	?	?
Burrowing	?	?
Fighting	?	?
Migrating	?	?
?	7 days	?
?	18–22 days	?
?	40–120 days	?
?	?	Adrenal
?	?	Pituitary
?	?	Thyroid
?	?	Parathyroid

CONSTRUCTIVE ACTIVITIES

With this work on the simpler forms of spontaneous behavior as a basis, we may now single out for study the more

complicated and specific performances of the rat, such as burrowing, gnawing, nest-building, and social activities. At the present time nest-building is the only constructive activity which has been quantitatively studied. We may ask, then, what it is that makes the rat build nests. In order to answer this question we must arrange our experiment so that nest-building is practically the only outlet

FIG. 39. RECORD SHOWING THE THIRST RHYTHM OF AN ADULT ANIMAL
Time in hours below

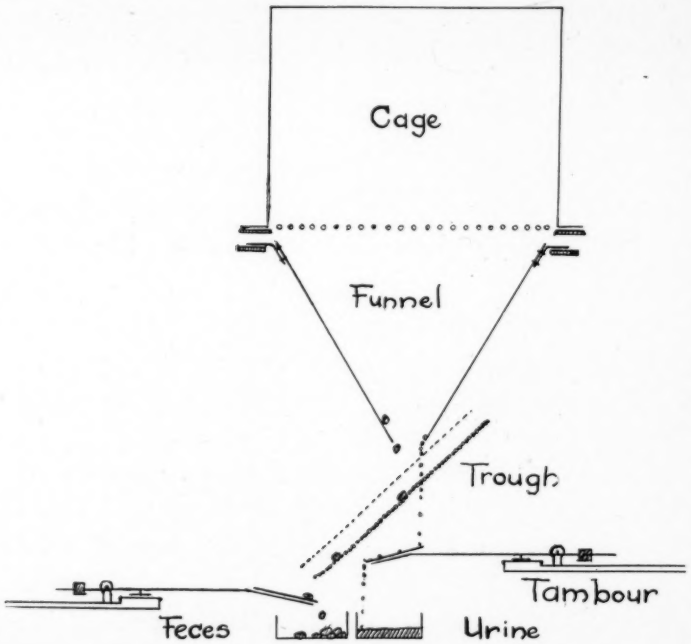

FIG. 40. DIAGRAM OF THE APPARATUS USED IN RECORDING URINATION AND DEFECATION RHYTHMS

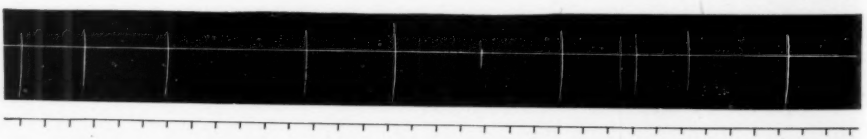

FIG. 41. RECORD OF THE DEFECATION RHYTHM OF AN ADULT RAT
Time in hours below

for the animal, and all other activities are either kept constant or eliminated. Such a situation in which spontaneous nest-building can be measured has been worked out very satisfactorily by Kinder (1927), in two different types of cages.

vals tell us nothing about the mechanism involved. Observed over long periods of time under controlled conditions, will it also be periodic like the running ac-

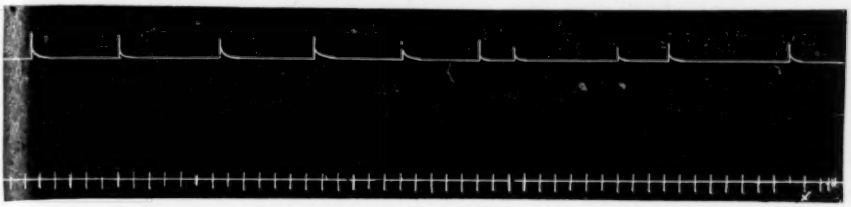

FIG. 42. RECORD SHOWING THE URINATION RHYTHM OF AN ADULT RAT
Time in half-hour intervals

In these cages the activity is measured in terms of the number of strips of crêpe paper used each day by the rat in building its nest. The method of presenting the paper differed in the two types of cages. In the first type 600 strips, ½ inch wide and 6 inches long, were scattered each day evenly over the floor, and the animals built their nests by pushing the strips into heaps. In cages of the second type, (fig. 43 *A* and *B*) 250 strips, 12 inches long, were hung over the sides so that the animal had to pull down one strip at a time and take it to the nest. With these cages Kinder found that if the nests are removed each day rats of all ages will build a fresh nest within the following twenty-four hours. That the activity is present and equally strong in both sexes is shown by the records of the daily nest-building activity of a male and female given in figure 44 *A* and *B*. Moreover, nest-building is practically independent of experience, since young rats thirty days old raised in sawdust build perfect nests out of the crêpe paper the first time it is presented to them. But what is it that drives the rat to build nests? Again observations for short inter-

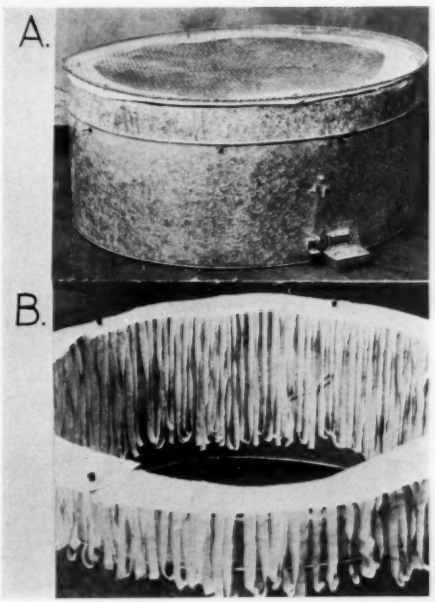

FIG. 43. PHOTOGRAPH OF ONE TYPE OF CAGE USED IN MEASURING NEST-BUILDING ACTIVITY

A shows the cage assembled without nest-building material. The walls are of galvanized iron and the top of wire cloth. The diameter of the cage is 36 inches and the height 18 inches.

B shows the arrangement of the strips of crêpe paper over the sides of the cage. The strips were hung so that the rats could reach them comfortably only by standing on their hind feet. (After Kinder, 1927.)

tivity? Here Kinder found that the four-day rhythm of the female is present just as it was in the running activity (fig. 45), but it has a very different relation to the cycle. Nest-building is greatest in the dioestrous interval of low running activity and lowest during oestrus when the running activity is highest. At parturition and during lactation the nests are very large, but the controlling mechanism is obviously not an essential part of the reproductive activity since the males often built nests as large as those of the mother rats.

Kinder found that all phases of the nest-building phenomenon have one feature in common that indicates the origin of the activity: every phase can be understood as a part of the heat-regulating mechanism by means of which the body-temperature is maintained at a constant level. The activity increases in low temperatures and decreases in high temperatures. It is high when there is a tendency for the body temperature to decrease, before puberty, during the inactive dioestrous interval, during pregnancy and lactation, and during starvation; it is low at oestrus, when the animal is very active and the body temperature tends to increase.

We may regard nest-building as a part of the heat-regulating mechanism, just as

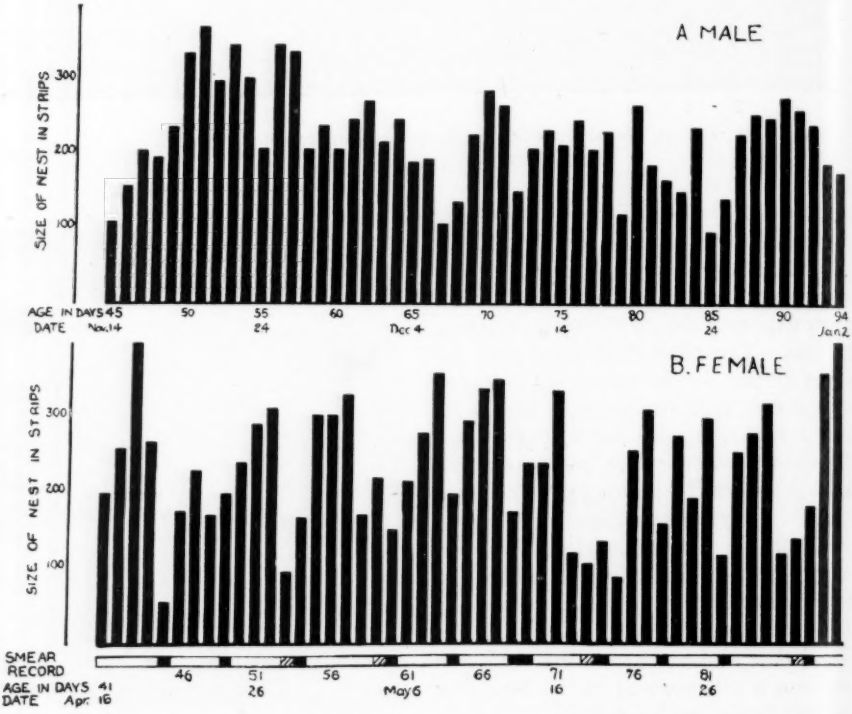
A MALE
SIZE OF NEST IN STRIPS
300
200
100
AGE IN DAYS 45 50 55 60 65 70 75 80 85 90 94
DATE Nov. 14 24 Dec 4 14 24 Jan 2
B. FEMALE
SIZE OF NEST IN STRIPS
300
200
100
SMEAR RECORD
AGE IN DAYS 41 46 51 56 61 66 71 76 81
DATE Apr. 16 26 May 6 16 26

FIG. 44. DAILY RECORDS OF THE NEST-BUILDING ACTIVITY OF *A*, A MALE, AND *B*, A FEMALE, OVER A PERIOD OF 50 DAYS

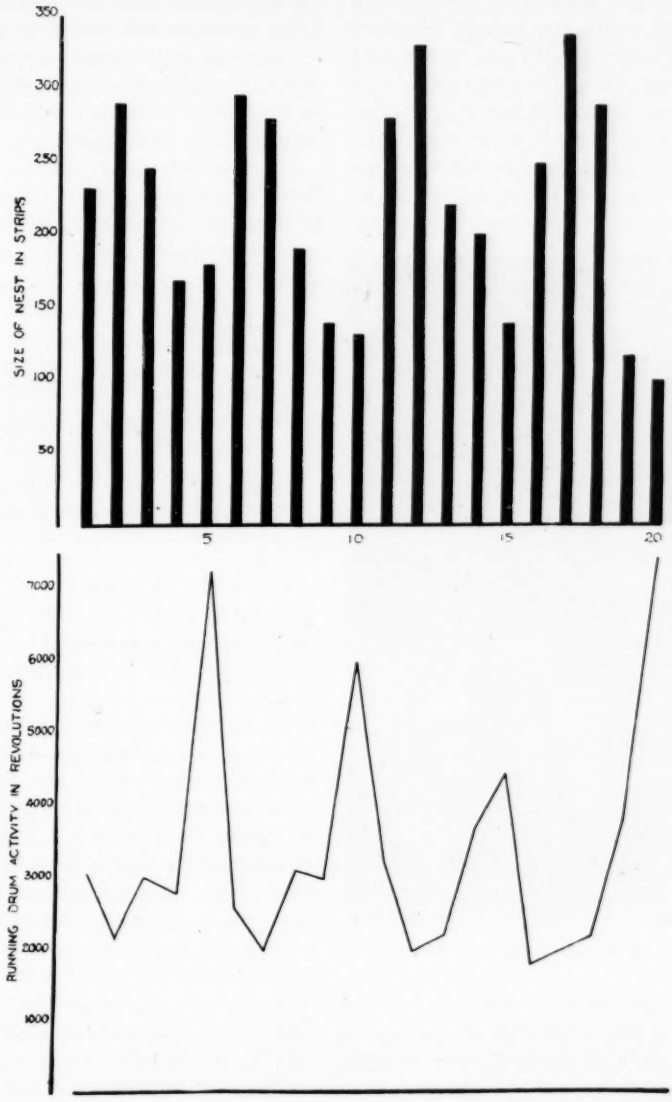

FIG. 45. RECORD SHOWING THE RELATION BETWEEN NEST-BUILDING AND RUNNING ACTIVITY (After Kinder)

we consider the growth of fat and hair during cold weather a part of the more primitive physiological manifestations of heat conservation. Nest-building, like the building of shelters and the wearing of clothing, is a much more highly developed method of maintaining a normal body temperature, but it is nevertheless an expression of the same impetus that produces the increase in fat and hair in more primitive animals (Martin, C. J., 1901). The mechanism of the drive involved here, therefore, is very different from that present in either the hunger or the sex activities.

FIG. 46. MULTIPLE ACTIVITY CAGE

Allied to nest-building in the rat are probably burrowing, the tendency of the animal to wedge itself into small spaces with contact on all sides, and its desire to huddle together with several of its mates. These activities also tend to conserve heat, in contrast to running, climbing, and jumping, which contribute to the maintenance of a constant body-temperature through heat production.

The various performances which, although associated with other drives, may be considered as contributing to the heat-regulating process, can be grouped as follows:

Nest-building Burrowing Huddling into small spaces Huddling together—social contact	conserve body heat
Running Climbing Jumping	increase heat production

Thus far we have investigated the different activities of the rat separately under more or less isolated and controlled conditions. We believe that it is possible, however, to study the animal under normal conditions, when it can indulge in any of the activities present in its usual outdoor environment. For this purpose we have constructed the set of cages shown in figure 46, in which a record can be obtained of the time spent each day by the rat in climbing, running, burrowing, gnawing eating, drinking, and mating. This cage makes it possible to account for the activity of the animal each day during every minute of the twenty-four hours. The large triangular central cage and all of the smaller cages at the side, except the revolving drum and the climbing tower, are supported on tambours. Running activity is recorded both graphically and with a cyclometer; climbing activity, by counting the number of times the animal goes up and down the tower each day. Both the entrance to the

tower and the top part are supported on tambours, so that a record is made on smoked paper each time the animal starts up the tower and when it reaches the top.

Because of the fact that we had only one cage we were not able to gather enough data to be of statistical value, but we have made sufficient observations to know that with some refinement of this method the behavior of the rat can be thoroughly studied in the laboratory. Certainly with this type of cage we can obtain a normal environment for the animal, in so far as it has an outlet for most of its different drives, and if we can judge how normal the environment is by the type of rat that it produces, the success of the method is unquestionable. An individual brought up in the multiple cage is far more intelligent than one raised in the ordinary running cage. Within the multiple cage the animal shows all kinds of constructive and imaginative activities, rarely, if ever, seen in an ordinary laboratory rat, and on occasions when it escapes it avoids recapture with extraordinary success. We may note in passing that were rats of this environment used for experiments on extirpation of the different areas in the cortex of the brain, much more noticeable defects in behavior might possibly be demonstrated as a result of the injuries than have appeared thus far in the rat kept under the usual laboratory conditions.

Individual differences are quite striking in the multiple cage if we may judge from our small number of animals. One rat will spend most of its time in the climbing tower, passing up and down as many as thirty or forty times a day; another will spend all of its time in the sex box; and another will gnaw all day long. None of our records have been taken over sufficiently long periods to permit us to give any perspective on either the constancy and fluctuations or the importance of the different activities in the life of the rat, but we do know that in this cage the running activity in the drum is reduced in every case to a few hundred revolutions per day. It is very interesting also, that in these cages where the animal has many different diversions the frequency of its eating period is greatly reduced. It enters the food-box once every five or six hours, and sometimes even less frequently, but whether it actually eats less food we have not yet determined.

That even the most complicated form of the rat's behavior may be studied in this cage is brought out by the following observations. In experiments on one animal a liberal supply of building material,—sticks, rope, stones, and cloth,—was placed in the large central cage. This animal had habitually deposited its feces in the water-cup. Usually the water was changed every day, but on one occasion, by some neglect, it was not changed for several days, so that the resulting odor became very unpleasant. At this point the animal started to cover the hole over the water-cup. It first removed part of the upper layer of the cardboard bottom of the large central cage, and dragged it into the water-box. It placed the cardboard over the cup and smoothed it down on all sides until the hole was perfectly covered. Then from the bottom of the central cage it lifted stones larger than its head three inches into the drinking cage and placed them over the cardboard cover. Besides the large stones numerous pebbles and sticks were used until the water-box was completely blocked. The animal had cut off its only water supply by this performance. Since we wished to see what it would do when it became very thirsty, the material was left undisturbed and no other water was given. After three days,

the animal pushed all of the sticks and stones from the drinking cage into the large central cage, tore up the cardboard seal, and drank its fill of the polluted water. This observation is certainly comparable to those made in the field. Had our apparatus been working better just at this time we should have obtained a complete biological record of this very interesting incident.

Another performance likewise constructive but less complicated was frequently observed. The rats plug up the entrance to any of the smaller cages whenever they have been frightened on entering them. This is the only explanation that can be offered for the frequency with which adult rats closed the entrance to the running drum shortly after they were placed in the cage. In one instance the opening was plugged up so tightly with nest-building material that a knife had to be used to open it up again.

Many similar examples could be given to demonstrate that in our artificially constructed environment practically every variety of behavior observable in a natural environment is obtained. And with a record of the way in which the animal spends its time before and after such episodes much more light will be thrown on their origin.

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THE CHIASMATYPE THEORY OF JANSSENS

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AMONG the many efforts made in recent years to establish a relation between structural conditions in the germ cells and genetic phenomena appears the case of Janssens' chiasmatypy as an explanation of "crossing-over" in *Drosophila* and other organisms. Morgan and his students have found the physical conditions, assumed to exist in chiasmatypy, suggestive of the mechanism required by the recombinations within the linked character groups observed in experimental breeding, and, so far, this is the only suggestion that has come from cytology to aid the geneticist in this significant problem. Just because of its importance in that application, the chiasmatype interpretation has acquired an interest much beyond what it would have had merely as an explanation of certain conditions occurring in the chromosomes during meiosis. It is true that, in its latest form, chiasmatypy becomes transformed into a theory that there are many ways by which, in one meiotic division, both equational and segregational separations may occur in the chromosomes; but this is merely an extension of the primary conception of Janssens that, in a particular manner, individual pairs of chromosomes may experience mutual interchanges of homologous elements. Since it is only in this more limited aspect that it has had extensive genetical application, it remains a conception which can be put to the test of direct observation on the chromosomes. It is proposed to submit Janssens' exposition to such an examination here.

By a most unusual coincidence the latest presentation of the case of chiasmatypy is based upon phenomena apparent in two genera of Orthoptera with which I have been intimately familiar for many years—*Mecostethus* (*Stethophyma*) and *Stenobothrus* (*Chorthippus*). Also I have studied with much care the cells of *Batrachoseps*, the form upon which the original conception was founded. This review is therefore incidental to a more comprehensive study, particularly upon *Mecostethus*, whose publication will supply many details which, although important to a thorough understanding of chiasmatypy, cannot be given here. Fortunately it is possible to resolve the complicated presentation of Janssens into a few simple elements, the consideration of which will be sufficient, I hope, to make a judgment possible.

ELEMENTS OF THE CHIASMATYPE THEORY

First, it would seem best to present the case as it was outlined by the author in his early paper. This may be done in the following statements:

1. There are certain phenomena in the first spermatocyte anaphase which are difficult to reconcile with the hetero-homeotype theory.

2. These suggest movements and translocations which involve the internal reconstruction of the chromosome.

3. If there were no such internal reconstruction of the chromosome there would be no occasion for two maturation divisions—a pure homeotypic mitosis,

added to a qualitative division, is entirely superfluous and without significance.

4. Added to this is the fact that maturation produces always four gametes, which, however, according to the hetero-homeotype theory, are of but two kinds. There seems to be no explanation of four gametes unless they are individually different.

5. There is no explanation of the pachytene stage by the hetero-homeotype theory.

6. The strepsitene stage is without explanation unless some change is accomplished during this long period.

7. While the hetero-homeotype theory supplies explanations for some phenomena of Mendelian inheritance, it fails in others because there are cases where there are a greater number of allelomorphic characters than there are pairs of chromosomes.

8. That which particularly characterizes the heterotypic chromosomes is their longitudinal cleavage in anaphase. Such a cleavage could not occur for various reasons given.

9. It is not probable that dyads (tetrads) come from a simple twisting of individual chromosomes, anatomically independent.

10. Various forms of chromosomes contradict the assumptions of the hetero-homeotype theory.

11. The alternative of a longitudinal division of the chromosomes in the metaphase of heterotypic division could not be realized under the conditions.

12. The only explanation consistent with the facts is one which realizes the occurrence, in one division, of both an equational and reductional division within the single chromosome.

As this summary indicates, Janssens' approach to a solution of his problem was largely from the *a priori* standpoint—to account for certain anaphase figures, to explain the tetraspore, to make understandable the maturation divisions, to make more applicable than the hetero-homeotypic theory does the phenomena of maturation in an interpretation of Mendelian heredity, etc., something must happen in the chromosome. In search for this peculiarity Janssens notes the strepsitene stage and sees in it a figure making possible the occurrence of both an equational and reductional division within one chromosome during a single mitosis. The relations of the homologous members of a chromosome pair, as found in the strepsinema, represent in a fundamental way the ones which are held to obtain in all the multitudinous forms of chromosomes in the phases of meiosis. This is represented diagrammatically by Janssens ('09) in figure 1, of which he gives this explanation:

> We shall in this caption style as *dyads* a couple of chromosomes in strepsinema a little before the time of formation of the spindle, ~~Schema I, *dyad*, C, *chromosomes*.~~ We shall call *filaments* F the two chromosome-threads resulting from a longitudinal cleavage of one of them. The place where the two chromosomes of the dyad cross we shall designate as a *chiasm* or *knot* N; a *loop* or "*internode*" B is formed by the two chromosomes between two knots; finally, a *segment* is the part of one chromosome included between two knots or chiasms.

Although it is not thus stated in the description, the diagram is so constructed

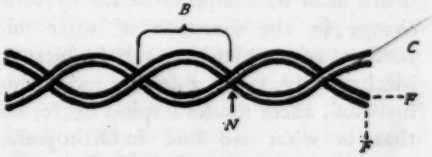

FIG. 1. THE BASIC FIGURE IN JANSSENS' PAPER, WHICH IS DESCRIBED IN THE ACCOMPANYING CAPTION

as to show that while the two chromosomes twist about each other, their chromatids ("filaments") lie as though projected in a single plane. Unless there were such a differential orientation, there would be no fixed positions for the chiasms, for these would be mere chance optical effects depending upon the point from which the twisted threads are viewed. It is not apparent, however, in any consideration of this matter by Janssens, how this precise arrangement is brought about.

Even if, for the moment, this matter of a specific and differential orientation is disregarded, there still remain a number of pertinent questions regarding the significance of the spiral condition in the

chromatin thread. Is it characteristic alone of the prophase stage of the first maturation, or is it a common disposition of the chromatin in prophase? If it is not unique in meiosis, what modification occurs that makes it so at this time?

In answer to the first question it must be said that the spiral form of the chromosome is a common condition of the prophase and appears to be the resultant of the rapid elongation of a thread within a limited area. The spermatogonia of the Orthoptera show very beautiful examples of spirals, as has been described by Sutton, Pinney, Wilson, Wenrich and others. In such cells the chromosomes extend across the nucleus and their ends are fixed at opposite sides. Under these conditions any increase in the length of the chromosomes must be compensated for by some change in the direction of their mid portion, often within a tubular vesicle. Mechanically, when a flexible rod is thus involved, there results a spiral figure, and that is what we find in Orthopteran spermatogonia. It is difficult to imagine any special significance in this particular spatial arrangement of the chromatin thread.

Janssens, however, sees in the first spermatocyte a condition which renders the strepsinema of highest importance for there, he assumes, two spirals twine about each other. How this relation is accomplished in such a manner as to be significant in the production of chiasms is not fully explained. Indeed, in his work on Orthoptera, the strepsitene condition seems to assume a minor rôle. It is not raised as a topic for discussion in the part dealing with *Mecostethus*, it is mentioned as a stage in the spermatogonia of *Chorthippus* but with no reference to its significance, and it does not appear as a topic in the outline of the general discussion. Among the very numerous diagrams explaining the assumed permutations of the chromosome parts ('24) only a few, mostly among the later ones, show the long familiar twisted threads. A careful examination of these, moreover, betrays the fact that some have taken on a new aspect and, instead of representing two intertwining spirals, merely show two superimposed split threads zig-zagging back and forth over each other in simulation of the strepsinema (Diagram IV). Even in the original presentation of the theory ('09) aside from figure 1 we see no more of the twisting pair of split threads, curiously placed so as to show the loops and splits in one plane, but instead a connected series of rings placed successively at right angles one to the other (Diagram XI). This is also the case in the paper of 1919 (Diagrams II, III) the only representation of the original conception being a figure copied from Wilson.

JANSSENS' EXTENSIONS OF HIS THEORY

In this preliminary paper we are promised, by inference, an explanation of how these "profound modifications of inner structure" are produced, but no convincing demonstration appears in the voluminous discussion of 1924. One is forced to conclude that the strepsitene condition gradually lost its suggestiveness and was replaced by another which had as prime features the following elements: (1) Any two homologous chromatin threads coming in contact may fuse and produce chiasms, permanent or transitory; (2) these contacts may occur face to face, in which event fusions may form between both members of the split threads, or edge to edge, when a chiasm is produced between only two of the four threads; (3) these fusions almost never take place immediately at the ends, but commonly near the proximal end; (4) by subsequent breaks at these points of permanent fusion,

new combinations of chromosome elements are made by exchanges of homologous parts; (5) these altered chromosomes are passed into the mature germ cells to become functional members of the nuclear mechanism. According to Janssens' own statement

> These segments, *and this is the very essence of chiasmatypy*, [my italics] interchange between allelomorphic chromosomes. These exchanges are made during the various stages of the maturation mitoses. ('24, p. 252).

The primary conception of an internal reorganization of homologous chromosomes by an interchange of like parts is maintained, but the method of its accomplishment is differently conceived. As the second sentence of the above quotation shows, the time at which chiasmatypy takes place has been extended to include the whole period of the maturation mitoses. This same idea is expressed elsewhere in these terms ('24, p. 258):

> We therefore often see, and at very different periods, chiasmatypies, complete as well as incomplete, indicated or finished. We draw from them no conclusion as to the exact moment when chiasmatypy begins or is completed. It is evident to us that it is produced at variable periods of meiosis and that there is no one moment peculiarly favorable for its production.

Finally, quite carried away with his idea, Janssens takes the final step and announces that any differential division, as between the equational and segregational form, within one mitosis is essentially chiasmatypy. Thus, in summing up the work on *Mecostethus* ('24, p. 196) he says:

> The two cases are not, strictly speaking, chiasmatypy, but they prove that the same mitosis may be, although for different chromosomes, at the same time equational and reductional, and this is the very essence of the theory which we defend.
>
> Thus we shall consider that very important fact from this point of view. It is moreover the first time that it has been pointed out.

As in so many other instances, Janssens quite overlooked previous announcements of his discoveries. The occurrence of equational and segregational division of different chromosomes in one meiotic division was described in the Orthoptera in 1905 (McClung), was demonstrated very fully by Wenrich in 1916, and was, at least by inference, described by Montgomery (1906) and by Wilson (1912) in the Hemiptera, where the X-chromosome divides sometimes in Meiosis I and sometimes in II.

Thus the original belief in a particular kind of internal chromosome reconstruction, by means of chiasms between twisted threads (as an explanation of peculiar conditions of first spermatocyte anaphase chromosomes and to meet certain theoretical difficulties of the hetero-homeotype theory), becomes a theory to explain any sort of combined equational and segregational action of a single mitosis. Notwithstanding the extension of the theory in this way, the principal basis still lies in the original figures of the first spermatocyte prophase, and an estimate of its value can best be gained by a detailed examination of these.

DO CHIASMS REALLY OCCUR?

It may be said at once that if Janssens' primary assumption be admitted, namely, that crossing threads in first spermatocyte prophases represent real chiasms, then all his numerous figures are possible, although this is not the only alternative. To enter into an analysis of these multitudinous configurations would be a waste of time—the essential thing is to discover whether the optical effect, so clearly evident in the cells studied by most investigators, upon which Janssens' interpretation rests, accords with his conception. We are not to discover whether chiasms are physically possible, but whether they do in fact

occur as described. It is most truly in this case not a theory but a condition that confronts us. Put concretely, the question becomes: "Do the structural elements of the maturation chromosomes, after they have become defined in the first spermatocyte prophase, maintain their integrity, or are they broken up and subjected to chance reconstruction?" In considering the problem, the fact, established genetically, that there is a reconstitution of the material units of hereditary processes must not unduly influence us, for the question at issue is not whether such changes happen, but, specifically, whether the mechanism described by Janssens is the one which actually exists. The test is, therefore, objective and observational and not speculative in character. It involves the use of the finest discriminative judgment in the interpretation of microscopical images, backed by a wide knowledge of the range and character of form variations of the chromosomes within the type of cells studied.

Janssens' knowledge of Orthopteran germ cells was apparently derived very largely from personal familiarity with only the two species described in his paper. The paper was written with slight reference to the large amount of literature on Orthopteran spermatogenesis and when notice is taken of this it is commonly in the form of notes which modify slightly, if at all, the form of opinion already expressed. Among neglected items of great significance bearing upon the problem with which he was concerned, and which are matters of record, may be mentioned (1) the almost universal occurrence of telomitic chromosomes in the Orthoptera; (2) the demonstration that the atelomitic chromosomes of *Chorthippus* are unions of non-homologous telomitic ones; (3) the fact that fiber attachment is practically a fixed structural chromosome feature; (4) chance-segregation and recombination genetically demonstrated by heteromorphic pairs; (5) the relations of homologous chromosomes in the tetrads and the sequence of their division demonstrated by unequal pairs; (6) the simultaneous occurrence of segregational and equational divisions of different chromosomes in one mitosis.

In extenuation of the errors and omissions in the work of Professor Janssens, it should be noted that war time conditions made it impossible for him to become familiar with many of the investigations reported from other countries. Further, during the completion and publication of his long Orthopteran paper, he was seriously ill with the disease which later terminated fatally. The contributions of Professor Janssens to biology were extensive and valuable, and it is a pleasure to me to express here an appreciation of him. We all delight to do honor to the memory of one who so sincerely and industriously sought to advance our knowledge in a field beset with many difficulties. In the same measure that he himself critically strove to understand the message written on Nature's page, we may be assured, would he wish others to appraise and judge the record which he has left. Since the conception of chiasmatypy is entirely that of Janssens, no consideration of it can escape an evaluation of the objective evidence he presented or of the attitude and methods which were his. Since the propounder of the theory can no longer defend his position I shall do my utmost to see that his views are correctly presented.

DIFFICULTIES OF INTERPRETING MICROSCOPICAL OBSERVATIONS

Admittedly, the conditions present at the time when the presumed changes of chiasmatypy take place are the most

difficult of interpretation of any found in the history of the germ cells. This is true in all cases. Even the comparatively large cells of the Orthoptera are really small bodies. Within these their very much more minute parts pass through most complicated evolutions. We are endeavoring to form a coherent picture of processes rendered static in their various stages. This would be hard enough for objects of ordinary size, but when it is attempted under a magnification of 3,000 diameters, with light passing through the masses instead of being reflected from their surfaces, and with only slight stereoscopic effect, it becomes exceedingly difficult. Within the narrowly limited mass of the cell lies its spherical nucleus, and in this space 23 chromosomes are distributed in such a manner as to approximate an even distribution in the first spermatocyte prophase. Naturally they present different aspects, according to their position, and often they overlie each other. Viewing the nuclear sphere with its constituent chromosomes, the observer must interpret the picture of two dimensions in terms of three. In diakinesis the formed chromosomes have much the same individual configuration as they show in the immediately subsequent metaphase, but at this time their chromatids are clearly distinguishable. Here Janssens found many of the figures upon which he based his views of chiasmatypy. It must always be remembered that when the fine, closely placed threads seem to intersect it is a matter to be decided, not directly observed, whether they do or not. To some extent the stereoscopic vision of modern binocular microscopes adds a measure of observational assurance to interpretation, but in the final analysis the judgment of the observer is the decisive factor. In the leptotene stages there is an apparently inextricable tangle of threads, but this becomes understandable when related stages are considered.

It is the great range and intricate character of chromosome movements, however, which renders difficult an appreciation of what actually happens within the narrow confines of the nucleus. A short, compact chromosome of an anaphase becomes first a vesicle with its chromatin uncertainly distributed and then a thin moniliform thread of relatively great length. Accompanying these physical changes are differences in reactions to stains which make identification of substances uncertain. Difficult as are the conditions there comes an element of assurance in judgments formed when the order and precision of movements are considered. Through the wide extent of plant and animal cells that have now been studied, the same procession of changes, individually varied in detail, to be sure, presents itself. We are confident of the reality and extent of the phenomena, but less assured of our intimate knowledge of them.

Partly this is due to an imperfect appreciation of the exact physical state of the materials whose set images we study. The undoubted gels and sols become translated in our thinking into the solids which the technique preserves in our preparations. We know now, even at this stage of microdissection studies on cells, that the protoplasmic differentiations which appear in their parts are not solids, but active, flowing, streaming and diffusing colloidal aggregates. Only when we think in the actual terms of physical structure can we appreciate the real character of cellular phenomena.

There comes, therefore, the need of translating in our thought the fixed pictures of apparently solid structures, into the real images of living, moving cellular elements. The chromosomes, which sometimes seem to stand apart from

nuclear connections, must be visioned as denser centers within a continuous medium. In most stages of meiosis the substance of the chromosomes merges gradually into the karyoplasm with varying gradation—only in metaphases do they present sharp limits. Even here, in preparations of highest technical excellence, their continuous relations are observable, and the dimensions of the chromosomes vary within narrow limits according to density and character of stain.

The outstanding difficulty in the chiasmatype interpretation, however, is the one already referred to—that of picturing the relations of structure as they lie superimposed in the line of vision. The two dimensional figures which appear as Janssens' version of "chiasms" are exactly the same in outline as those of other investigators who see no evidences of chiasm but only crossing threads. What happens at the apparent intersection is not directly observable, but must be conceived by putting together images of the same related threads as viewed from different angles in many chromosomes. There must be such a consistency of image thus derived as would result if one could actually take out a single chromosome and view it from every possible point.

MANNER OF SPLITTING OF CHROMOSOMES

Contributing to misunderstanding also is the fact that Janssens fails to comprehend the true nature of the first spermatocyte prophase chromosome. To him it is not a tetrad but a dyad. (Incidentally Janssens' use of the term *dyad* for a geminus or bivalent chromosome is incorrect, since it signifies the number of chromatids in a chromosome which is in mitosis and not the number of chromosomes in a multiple.) At some time and in some way a longitudinal cleft appears, but the chromosome is still a dyad. About the time and manner of the appearance of the longitudinal split Janssens is very uncertain, as indicated previously in the quotation given on page 347 and in the following extracts from his paper published in 1924:

> Near the beginning of the diplotene stage one sees here and there, at certain points on the chromosomes, a longitudinal cleavage appear which corresponds to the cleavage in the prophases of the spermatogonial mitoses. (p. 182).
>
> . . . . these fusions ("permanent" fusions in the dyads of *Stethophyma*) are very primitive and they were already observed in chromosomes which do not yet show the slightest tendency toward splitting. (p. 184).
>
> Toward the end of the strepsitene stage one sees clearly a second cleavage appear in each of the branches of the strepsinematic couples. (p. 217).
>
> It is certain that in *Stethophyma grossum* the fusions at points of intersection are produced at a very young stage and one which corresponds to the leptotene in the species where the pachytene is observed. It is quite possible that in these cases we have a complete chiasmatypy on account of the chromosomes not yet having undergone longitudinal cleavage (which is produced, however, often in slightly advanced prophases). (p. 253).
>
> If we have not spoken of the formation of chiasmatypies at so early a stage it is not a reason for saying that it cannot be produced. W. Rees B. Robertson wrote the following sentence which, we believe, indicates the solution of the question and which is of a nature to permit us to agree perfectly: "My conclusions from the Tettigidae are that these spermatogonial chromosomes on entering synapsis are already split." p. 258. We must say in all truth that we have not yet succeeded in finding that before the pachytene stage (synapsis) the elements which conjugate are already split, but we admit willingly that it is thus in the subject studied by the author, and we find in this fact of "presynapsis splitting" a reason for admitting that incomplete chiasmatypies may be roughly formed before the pachytene stage. (p. 254).

Having failed to appreciate the character of the longitudinal split and being so strongly impressed with the significance of the spiral condition of the chromosomes at certain stages, Janssens quite overlooks the most important circumstance in the history of the meiotic chromosome, i.e., the

simultaneous existence of two planes of division at right angles to each other, *proceeding from opposite ends of the chromosome.* This relation was admirably and conclusively demonstrated by Wenrich in his careful study of the "selected" chromosome of *Phrynotettix.* In this species conditions are the same as in other Orthoptera except that certain chromosomes may be individually recognized, at all stages of meiosis, by peculiarities of form and behavior. Because of these circumstances depend the manifold forms of chromosomes found in meiosis I of animals and plants. These have repeatedly been described for many species and do not require extensive consideration here, but since an understanding of them is essential to a discussion of chiasmatypy a few of the more significant ones will be reviewed. I should first like to recall the case of the double *V*'s, so very evident, particularly in the Hemiptera. In these, the two splits, proceeding from opposite ends of

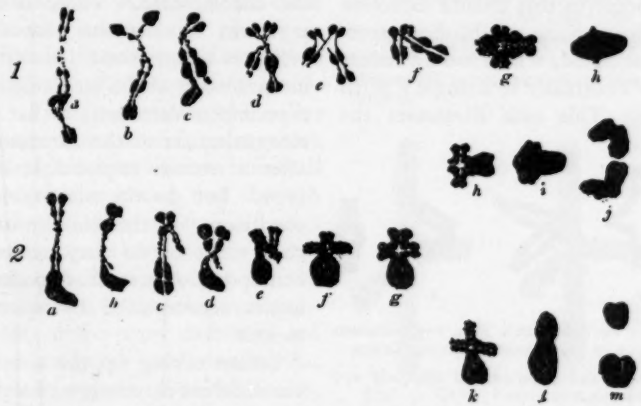

FIG. 2. COPIES OF WENRICH'S FIGURES 64 AND 65

Row 1 represents progressive stages of Chromosome "*B*" and row 2 of Chromosome "*C.*" In each the simultaneous appearance of the two clefts in planes at right angles to each other, and proceeding from opposite ends of the tetrad, is shown. The tetrad 1*e* presents a typical "chiasm" which is nothing more than the crossing of one chromatid over another.

the two planes of splitting in the tetrad are distinguishable and it is established, for these cases, that the equational split proceeds from the proximal end (that at which the fiber attaches) to the distal, while the segregational proceeds from the opposite end at right angles to the first (fig. 2).

ORIGIN OF CHROMOSOME FORMS

Upon the relative rate and direction of the movements of the four chromatids in relation to these two planes of separation the chromosome, at right angles to each other, extend completely through its length. The chromatids, remaining united by their ends, diverge along each split for as much as 90°, producing a variety of figures. If one of these, which presents two divergences of 45°, be viewed exactly in the plane of one split, it looks like a simple *V*. Rotated through 90° it would appear again as a *V* but with the direction of the opening reversed. Any intermediate position would display both *V*'s, one from the outside, the other from

the inside. Whenever thus obliquely viewed each double *V* presents the appearance of two *V*'s with their inner arms crossing. Such crossed threads Janssens figures as representing a chiasm. Obviously, in this case, the two chromatids are not in contact and could not fuse, but the optical appearance is not thereby affected. It is only necessary to imagine the *V*'s compressed parallel to the axis of vision to bring the apparently crossed threads into contact. But why should movement occur in this chance direction instead of in a plane established structurally in the tetrad, which would reduce the double *V* eventually to a single *V* with double arms? This case illustrates the essential weakness of Janssens' reasoning—it calls always for the operation of chance change against the inherent structural stability of the chromosome. While it may be regarded as extreme to instance the "chiasm" of the double *V* as illustrating chiasmatypy, the case does not differ in principle from the ones figured by Janssens (fig. 3).

FIG. 3. A COPY OF PAULMIER'S FIGS. 1–5, SHOWING THE STRUCTURE OF THE TETRAD IN ANASA TRISTIS

Chromosomes 3 and 4 are viewed obliquely and present apparent chiasms.

From this double-*V* figure can be derived all of the various forms of the first spermatocyte chromosome by modifications of (1) the amount of separation of the four chromatids along the two planes originally at right angles to each other; (2) the relative time of the separations of these planes; (3) the amount of extension or condensation they exhibit; (4) the position of the fiber attachment; (5) the persistence or loss of the endwise union of chromatid pairs; (6) the spatial relations within these chromatid pairs. The question of chiasmatypy resolves itself accordingly into one concerning the interpretation of chromatid relations. Janssens chooses to assume that continuity of chromatid is lost and mechanical reconstruction accomplished through reciprocal exchange of homologous chromatid parts. A new organization is set up in the chromosome. There is no *a priori* argument against this, for all evidence indicates unique conditions at this period in the history of the germ cells, and genetic experiments demonstrate that an internal reorganization of the chromosome occurs after a manner explainable by chiasmatypy. But do the observable structural conditions of the chromosome support that view, or do they accord with the conception of persistent continuity of elements accompanied by spatial readjustments?

Before taking up the consideration of the different chromosome forms let us first note that movements, varied and extensive, characterize the chromosomes in all mitoses. There are separations and recombinations, twistings and loopings, diffusions and retractions, and all manner of combinations of these. Like so many living organisms, the chromosomes, by their own intrinsic contractile power, carry through their ordered movements. In our efforts to interpret the fixed stages of these activities we must always bear in mind the nature of the living substance and the character of its movements. The chromosomes are not rigid, immobile threads or rods, dependent upon external forces and chance contacts for their resultant forms, but active, autonomous elements pursuing an ordered course through a most involved and intricate series of

changes. We are not here concerned with the cause of these movements, but only with their manifestations. An understanding of them is, however, entirely dependent upon a true appreciation of the conditions under which they occur. These phenomena I have studied in many scores of Orthopteran species and have compared them with the ones appearing in most of the classical objects described in the literature. In particular I have for many years studied intensively the meiotic chromosomes of *Mecostethus* as found in the three species, *lineatus*, *gracilis*, and *grossus*, as well as those in *Stenobothrus* (*Chorthippus*) and *Chloealtis*, where euchromosome multiples occur. I am thus intimately familiar with the particular material upon which Janssens based his conclusions, and shall be able to criticize them, not through remote analogies with other and uncertainly relative conditions, but by direct comparisons. A brief account of the synaptic process in *Mecostethus* was published in 1924 and a more extensive and comparative study of meiosis in this genus will soon appear. For this reason the present discussion will be confined as much as possible to details most pertinent to the immediate issue of chiasmatypy.

CROSS-SHAPED CHROMOSOMES

Two first spermatocyte prophase figures, in particular, are used by Janssens as the basis of his interpretation—the cross and the ring. These are common forms of chromosome in prophase and metaphase of Meiosis I of both plants and animals and their correct interpretation has many times appeared in the literature, but both have been erroneously described in several instances. It remained for Janssens to give an entirely new and almost fantastic account of their structure. The cross (fig. 4), according to Janssens, results from the following chromatid movements: (Diagrams III, V, VI, VII, VIII, '24) (1) two homologous chromosomes, longitudinally split, approximate *side by side;* (2) the two chromatids, laterally in contact, fuse at some non-terminal point and

FIG. 4. THE FORMATION OF THE CROSS-SHAPED TETRAD AS REPRESENTED BY JANSSENS IN DIAGRAM VI OF HIS 1924 PAPER

One homologue is represented in solid black, the other by dotted lines. A fusion between contiguous chromatids is assumed where the vertical line intersects.

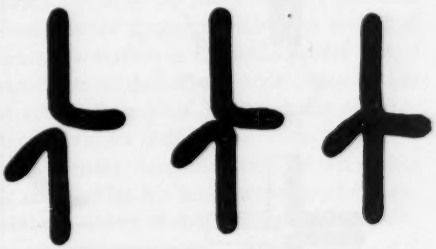

FIG. 5. CROSS FORMATION AS REPRESENTED BY JANSSENS IN HIS 1909 PAPER, DIAGRAM XVI

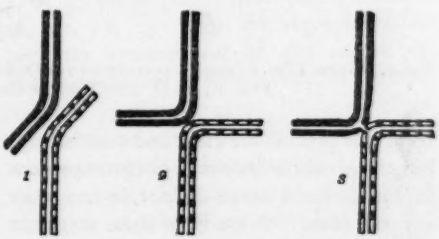

FIG. 6. EXCEPT IN DETAILS THE CONDITIONS HERE ARE SIMILAR TO THOSE SHOWN IN FIGURE 4

Copy of Diagram III of Janssens' 1924 paper

change their connection; (3) at the level of chromatid fusion the shorter arms swing each through 90° and come to lie at right angles to the axis of the longer members; (4) the longer arms may then

take a position in the same plane as the shorter, or not. A simpler method was described in the first paper ('09, Diagram XVI) (fig. 5), and again in 1924 (Diagram III). In this, two longitudinally split bent homologues unite laterally by their angles, where the chromatids in contact fuse and change their connections (fig. 6).

The result is the same as before—an exchange of equivalent segments between the homologous chromatids at the point of fusion. The diagrams given to illustrate this process are clear and convincing, but the accurate drawings of chromosomes in the assumed stage do not in any way support them. A study of these stages in the cells themselves shows nothing whatever to corroborate Janssens. I have examined hundreds of cross-shaped chromosomes, in all stages of development, not only in *Mecostethus* but in many other species, and I have never seen a single one which would correspond in its structure to the diagrams given by the Belgian cytologist. I have no doubt whatever of the error of his interpretation of this chromosome form.

Perhaps the best evidence as to the actual composition of the cross is given by the heteromorphic tetrads of *Phrynotettix* (fig. 2). It will be noticed that the chromosomes "*B*" and "*C*" may be constituted of unequal homologues, a circumstance which makes possible the exact identification of the two constituents. These are first seen lying parallel with each other, apparently unsplit, but shortly afterward a longitudinal division appears in each, beginning at the proximal end. Almost at the same time, the homologues diverge at the distal end, the shorter member leaving the longer. While the halves of the individual homologues produced by the division proceeding from the proximal end remain in parallel contact, the homologues move apart until they may lie extended in a straight line. The result is a cross-shaped chromosome with two splits intersecting at right angles—the one dividing both the small and large homologues rep-

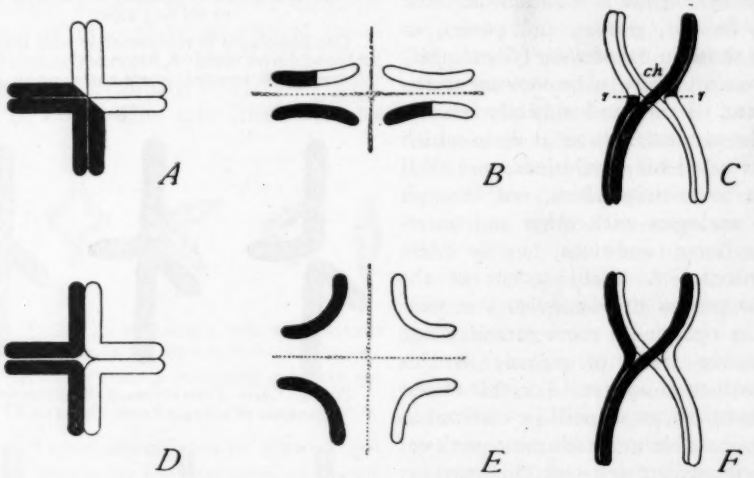

FIG. 7. WILSON'S FIG. 6 (1920) ILLUSTRATING THE DIFFERENCE BETWEEN JANSSENS' INTERPRETATION OF THE CROSS FIGS. A, B, D, AND THAT OF OTHER INVESTIGATORS, FIGS. C, E, F

resents clearly their equational division, while the other just as definitely marks the separation between the two homologues. In this case all the visible appearances confirm the interpretation, but Janssens, in discussing Wenrich's ('16) figure 62 of chromosome "*A*," disregards entirely the evidence presented for identification of the two planes, and, by substituting his own interpretation, distorts the figures into a support of his position. An oblique view of a tetrad in an early stage of the divergence of the homologues (Wenrich, fig. 64*e*) shows a double-*V* effect and the crossing threads, although evidently not in contact, become a chiasm to Janssens. Comparing the condition of the cross, as it actually appears, with Janssens' conception, these divergences may be noted: (1) the union of homologues is parallel and face to face and not at an angle and lateral; (2) union of chromatids is at the ends and not subterminal; (3) the chromatids continue unaltered from one extremity to the other and do not fuse (fig. 7).

An examination of Janssens' own figures in almost every case confirms the view opposed to his own (figs. 152 *c*, *d*, *e*, 183, 186, 187). The occasional instances of asymmetrical relations of the four chromatids at the center of the cross are easily understood and do not involve any breaking and recombination of elements. Those of the later first spermatocyte prophase, as in figs. 152, 153, are chromosomes still of a very loose structure in which none of the parts are clear and sharply defined. Those of the first spermatocyte metaphase, figs. 183, 185, 218, require more special mention because they afford a definite basis upon which to place an estimate of Janssens' judgment regarding conditions of chromosome structure. Fig. 183, chromosomes 6, 7 and 10, are quite symmetrical crosses viewed *en face* and give no suggestion of altered parts. Chromosome 5 of the same figure shows a very irregular and distorted appearance and obviously is not normal. Fig. 185, chromosomes 2 and 4 are clearly broken chromosomes such as may be found in any preparations that have suffered injury. Janssens recognizes their fragmented condition but, instead of appraising it properly, sees only an evidence that the break has occurred in a weak place which must be that at which the chiasm appeared. Chromosome 4 is broken not only at the presumed chiasm but also near the ends. All these clefts are beyond question pure artifacts. The long slender chromosomes of *Mecostethus* are easily injured in preparation and breaks of any character may be found. That Janssens should seize upon such obvious technical faults as evidences of fundamental reconstruction within the chromosome makes it very certain that his judgment of cytological values is not to be relied upon.

A similar demonstration of this fact is afforded by his interpretation of certain oblique views of first spermatocyte metaphase chromosomes. When they are viewed *en face* (fig. 182, chromosomes 1, 4, 7, 8, 9) or in polar view (chromosomes 16, 17, 18, 19) they are represented as perfectly symmetrical at the region of fiber attachment. Whenever they are represented in oblique view, however, their chromatid relations invariably are otherwise conceived, (chromosomes 2, 3, 13, 15, 21, 23). The drawings of chromosomes 21 *A* and *B* are revealing of the faults in Janssens' interpretation. Here a purely optical effect is converted into a structural relation quite alien to the real conditions as revealed by the history of the chromosome and by its appearance when viewed otherwise. This optical effect can be produced by varying the focus on any chromosome of homogeneous constitution and it differs according to the

angle at which it is placed in reference to the visual axis. But most convincing is the concordance between these chromosomes of *Mecostethus*, almost exclusively of one single type, as they appear in diakinesis, (with the four chromatids symmetrically placed in reference to the two prospective planes of division) and as they are later in the equatorial plate of the first spermatocyte metaphase (fig. 13. Janssens' figs. 186–191).

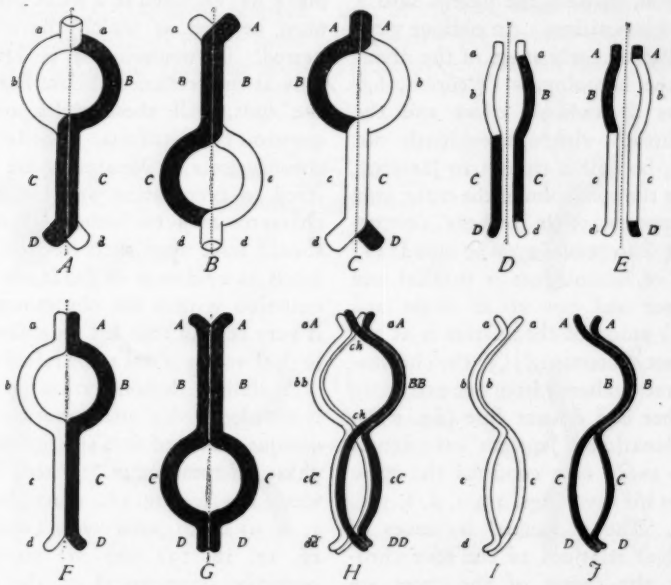

FIG. 8. THE DOUBLE RING TETRAD AS VIEWED BY JANSSENS, A, B, C, D, E, AND BY OTHERS, F, G, H, I, J

A and *C* are viewed at angles 180° apart, while *B* would represent the appearance at an intermediate position of 90°. At the points of intersection breaks are assumed by Janssens to occur, giving the results represented in *D* and *E* (Wilson's fig. 2 [1920]).

RING CHROMOSOMES

The ring chromosomes of the Orthoptera have been exhaustively discussed in many papers (McClung, '00, '02, '05, '14, '17; Sutton, '02; Wenrich, '16; Robertson, '08, '16; Granata, '10; Wilson, '12; and others) and a general agreement reached in regard to the method of their formation. It will be recalled that the process is a comparatively simple one in principle, as thus understood (figs. 8, 9, 10). The tetrad, at the beginning of diakinesis, is a rod, split longitudinally, in two planes placed at right angles. One of these represents the space between the homologous chromosomes of the pair, the other their coincident equational division plane. This is a brief stage, but it is clearly apparent in *Mecostethus* and is of unusual prominence in *Stenobothrus*. Janssens does not figure it at all in the former genus and is not clear in the representation of it in the latter. *Mecostethus*, of all the genera of the Acrididae studied, shows the least tendency to produce rings, so that it is not a good form in which to work out their development, but *Stenobothrus* is exceptional in the clearness with which

the details of this type of chromosome formation are shown, especially in the case of the multiple euchromosomes. Robertson has represented these stages with great care and accuracy in a series of drawings ('16, figs. 163–177). The multiple ring chromosomes are of unusual interest because they show, beyond question, the alternate separation, in successive regions, of the four more or less parallel chromatids along the two planes lying at right angles to each other. Under ordinary circumstances, it is not possible to distinguish between the two lines of these chromosomes see no alteration in the composition of the constituent chromatids but merely alternate approximation and divergence between members of given pairs. Janssens' conception is radically different. For him, the series of loops in multiple rings in diakinesis represents persisting loops from the strepsitene stage, with chromatids breaking and fusing with different partners at the "chiasm." The position of the loops at right angles is not a primary relation, but one secondarily acquired. As a result of these altered relations, the openings of alternate rings,

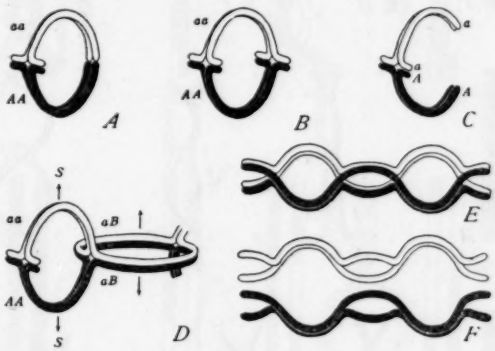

FIG. 9. THE STRUCTURE OF RINGS, SIMPLE AND MULTIPLE, AS CONCEIVED BY MOST INVESTIGATORS OTHER THAN JANSSENS (WILSON'S FIG. 3 [1920])

cleavage in a tetrad, but, in *Phrynotettix*, Wenrich was able to identify these definitely. The evidence here is that the two splits exist together and that separations of the chromatids in the two planes occur at the same time, but usually in unequal degree. Commonly, also, fiber attachment is so made that the first movements of the chromatids toward the poles of the spindle separate sister elements—an equational division. When chromosomes are long, multiple rings occur, and, as generally agreed, successive openings are placed at right angles to each other. With the exception of Janssens, observers of although in planes inclined at an angle of 90° to each other, are always the space between homologues and never between sister chromatids. In seeking a logical justification of this conception Morgan would assume that, e.g., the separation between paternal and maternal elements always occurs first and thus, as Wilson states, "makes the whole series of assumptions complete." But, as these authors imply, this merely adds another assumption to all those which have built up the chiasmatype structure. Unfortunately, it goes directly counter to the facts. As already pointed out in discuss-

ing the formation of the double *V*'s and multiple rings, the two clefts in the tetrad are present at the same time and proceed through the length of the thread or rod from opposite ends (fig. 11).

The cross and the ring are correctly regarded by Janssens as essentially the same in their formation—four chromatids, elsewhere divergent in pairs, approach and occupy a space equal to the sum of their diameters. The end of a ring chromosome or the place where two rings in a multiple join, if seen *en face*, appears as a cross (fig. 9). Viewed in this way such a chromosome should show one or more of the chromatids passing across from one side to the other, according to Janssens, but they do not do so and *none of his drawings of the actual chromosomes are shown in this position*. On the contrary, whenever chromosomes are thus figured with the four chromatids separate and visible, either in the first spermatocyte prophase or early first spermatocyte anaphase, the constituent elements maintain their positions in the same quadrants where they were found in the four strand stage. The only figures which may be regarded as even remotely supporting Janssens' position are those of broken, distorted or obliquely viewed tetrads.

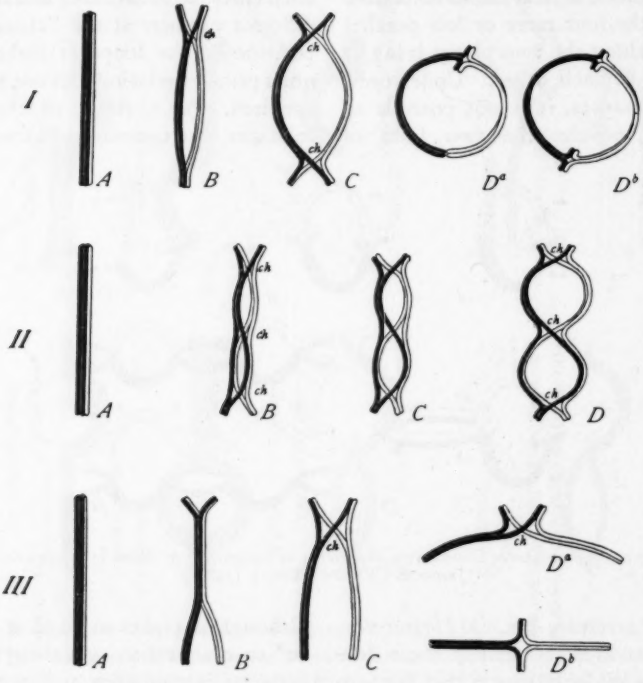

FIG. 10. METHOD OF RING AND CROSS FORMATION AS COMMONLY CONCEIVED (WILSON'S FIG. 5 [1920])
When obliquely viewed apparent chiasms, *ch*, appear in both forms. (Cf. III *C*, with 1*e* of fig. 2).

It thus appears that the chromosome forms most relied upon by Janssens as evidence for chiasmatypy are capable of

explanation in quite another and far more probable manner, which calls for no disruption of chromosome structure. Since this explanation was independently arrived at by a great many investigators, and since it is consistent with the structure of Janssens' presentation. The theoretical possibilities of movements between the four chromatids of a tetrad, assuming chiasms to occur, have been carefully and exhaustively explored by Wilson and Morgan in several publications. No better

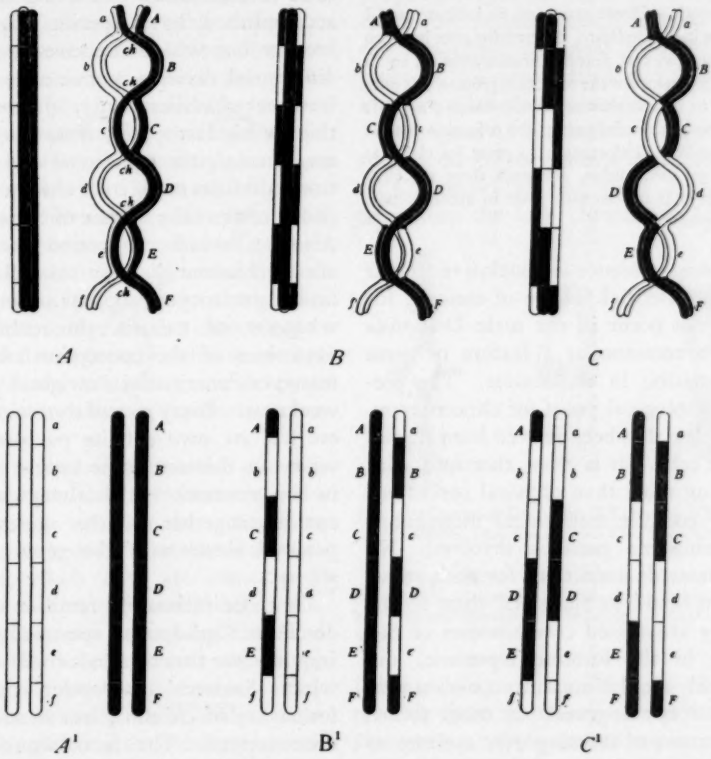

FIG. 11. MULTIPLE RING FORMATION AS COMMONLY UNDERSTOOD, *A* AND *A'*, COMPARED WITH JANSSENS' VIEW, *B* AND *B'*, *C* AND *C'* (WILSON'S FIG. 4, 1920)

In all these figures one homologue is shown in black and the other is white. Fusions and breaks at intersections produce, according to Janssens' view, the combinations shown in *B'* and *C'*.

of the chromosomes at all stages in their history, it must be assumed to be correct.

INADEQUACY OF EVIDENCE FOR CHIASMATYPY

It has been my intention in this review merely to consider the objective evidence for or against chiasmatypy in the light of Janssens' presentation. The theoretical possibilities of movements between the four chromatids of a tetrad, assuming chiasms to occur, have been carefully and exhaustively explored by Wilson and Morgan in several publications. No better presentation could be given and it would be useless to encumber the literature by further considering what might happen under circumstances which do not exist. Because of the need to find a structural basis for the suggested facts of chromosome reorganization, as exposed by the

"crossing over" of characters in genetical analysis, Janssens' seductive suggestion required careful study. It has had its day in court and been found wanting. According to Morgan's latest conclusions ('25, p. 123)

> The genetic evidence may seem to indicate, and I think that it does indicate, the crossing over between homologous pairs of genetic chromosomes is, so to speak, a by-product of the reduction process. It does not seem to be one that necessarily takes place. It may not be an essential part of the reduction process and it would be unfortunate to press its claim at present into other fields, although there are clear indications that it does take place in other animals and some plants.

The present evidence is conclusive that it is not an essential feature of meiosis, for it does not occur in the male *Drosophila* although common as a feature of germ cell formation in the female. The presumed cytological proof for chiasmatypy, nevertheless, has been derived from studies on male cells. It is clear, therefore, that something more than physical conditions making possible mechanical interchange of chromosome parts is involved. No more favorable conditions for such translocations could be imagined than in the minutely attenuated chromosomes of *Mecostethus*, in the forming leptotene, and presumably similar conditions obtain during the spermatogenesis of other forms, but instances of crossing over are rare or lacking in the Orthopteran male. Also, as indicated elsewhere, the obvious fact that during synapsis profound changes occur in the chromosomes, as indicated by the progeny of a single pair of parents, is no support of a theory which accounts for a particular kind of influence exerted after a specific manner. Evidence for the existence of change offers no argument for any one method of accomplishing it.

The term *chiasmatypy* was coined to designate the essential structural alteration presumed to occur in the meiotic chromosomes at a definite period of their development. It will merely confuse the problem for which the geneticists seek an explanation, to extend this idea of a structural reconstitution of the chromosomes, accomplished by a specific act, into a broader one which conceives any act of differential division in one mitosis as an instance of chiasmatypy. Janssens does this in his last paper, instancing, as already noted, the equational and segregational division of different chromosomes in one mitosis as the essence of chiasmatypy. Also he extends the period over which actual chiasmatypy may take place from first spermatocyte prophase to any period whatever of meiosis. In reality these extensions of the conception are just so many evidences of its original inherent weakness. Every step of the meiotic process has its own definite purpose—somewhere in this series the unique relations in life processes, which always mark the coming together of the maternal and paternal elements of the germ cells, are set up.

To those intimately familiar with the details of Orthopteran spermatogenesis it is quite clear that the basic condition upon which Janssens' conception rests, the formation of chiasms, has been entirely misconceived. The facts are otherwise than as reported—the "chiasms" are optical effects and not structural conditions. Thus we must conclude unless all other investigators are wrong and Janssens right. To the concordance of opinion in the past I must add the confirmation of my own judgment after extended and careful studies upon the same genera employed by the Belgian cytologist, backed by an extensive comparative knowledge of conditions in the Orthoptera as a whole.

THE NATURE OF THE CHROMATIDS

While, therefore, we must consider that the essential feature of chiasmatypy is due to a faulty conception resulting from misinterpretations of optical images, it is recognized that otherwise, with few exceptions, Janssens correctly represents in his figures actual conditions found in the cells. There are present the twists and turns of the first spermatocyte prophase chromosomes and the asymmetries in the chromosomes of first spermatocyte anaphase which first attracted his attention. How then can these be explained if not by the scheme of Janssens? To understand these conditions one must free his mind of many preconceptions regarding the physical nature of the chromosomes and regard them properly as living, active, viscous threads, exhibiting a wide range and varied character of intrinsic movements.

Also it must be appreciated that the unit in structure and movement is not a whole tetrad, or even its constituent homologous chromosomes, but the chromatids of which they are constituted. Herein lies another of Janssens' difficulties. For him there was something fixed and unchangeable in the tetrad unless by chance a break should occur and secondary connections between chromatids result. This is exemplified in a comment upon the interpretation of the multiple ring chromosome as represented in the figures of Granata, Robertson and others. The existence of twists, often asymmetrical or unequal, he regards as the best evidence against the view that such figures are produced by the opening out of four threads along planes at right angles to each other, for he says "the four filaments of a loop must be and remain parallel according to this supposition" ('24, p. 274). In reality the four chromatids, sometimes united only at their proximal ends, may exhibit almost all the configurations that could be imagined as the result of the somewhat free movements of this number of active, mobile bodies under the conditions set by the cell. In the later first spermatocyte prophase stages the extent of independent movement becomes much reduced and in the metaphase complete immobility appears to be reached in the apparently homogeneous chromosomes.

This state is succeeded with startling suddenness by movements in the anaphase which reveal at one time both planes separating the four chromatids (fig. 13,

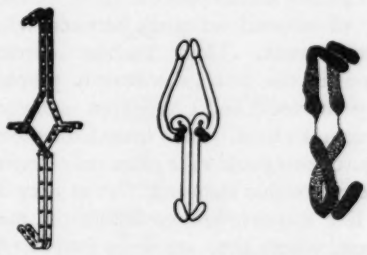

FIG. 12. COPIES OF DIAGRAMS XXIII AND XXVI *b*, OF JANSSENS' 1909 PAPER, AND FIG. 259 *y* OF HIS 1924 PAPER

Such appearances of asymmetrical relations in the chromatids of tetrads led Janssens to think of the breaking and recombining between chromatids in the tetrad.

Janssens, '24, figs. 186–193). In this manner there reappear the conditions of diakinesis. Even in *Mecostethus*, where uniformity of behavior is more nearly reached by the chromosomes than in any other Orthopteron, there are sometimes asymmetries shown by twists of the chromatids (Janssens, '24, fig. 191). Such phenomena are much more marked in batrachians, and apparently were the primary incitement to the chiasmatype conception. According to Janssens, only by breaks and recombinations could such relations between formed chromatids be brought about. For this idea of fixity in

condition, disturbed by uncertain and unpredictable accidents of contact and exchange, we must substitute the view which recognizes in the tetrad four separate, moving elements, which, at different first spermatocyte prophase stages, may variously orient themselves without loss of continuity or of primary relations. In this way all the curious and sometimes complicated chromosome forms receive ready and reasonable explanation. By its nature chiasmatypy could account only for relations between the parts of a single tetrad, but a proper appreciation of the real nature of the chromatids and their movements makes possible an understanding of unusual relations between whole chromosomes. Thus, annular chromosomes in the first spermatocyte prophase may interlock, and I have seen as many as three in a chain. Such interchromosomal adjustments could take place only between freely movable elements, just as they are, in like manner, broken before the metaphase, where they are never found.

An extensive review of late chromosome forms would hardly be appropriate in this place, but since consideration of these led Janssens to his views on internal reorganization of chromosomes it may be profitable to note a few typical examples. Diagrams XXIII and XXVI of Janssens' original paper of 1909 are representative of the conditions which so impressed him with the inadequacy of the hetero-homeotype theory and the need for a new interpretation. The first of these represents a view *en face* of an elongated early (fig. 12) anaphase cross with non-terminal fiber attachment. This condition is pictured in figure 259 *y* ('24). The lower limb presents a chiasm near the equatorial plate. Such a figure could result, argues Janssens, only by the fusion and recombination of chromatids at this point. In reality, all that has happened here is a rotation of the two chromatids around the lengthwise axis of the chromosome. The other diagram represents a chromosome of the same character in which rotation has occurred symmetrically, but in opposite directions, between the chromatids above and below the equatorial plate. This is a common condition in long chromosomes, such as the euchrosome multiples of *Chorthippus*, and like relations are represented by Janssens ('24) in figure 259 *e*, *j*, *r*, *t*. It is rather curious that Janssens, who was so much impressed by the rotation of chromosomes about each other in the strepsinema and in other stages, should so entirely disregard the evidences for similar movements between chromatids.

Such rotation of chromatids occurs also between the sister elements of spermatogonial chromosomes in the Orthoptera, and between those of somatic cells in a great many forms with long chromosomes, as for instance the Urodeles. The simulation of the assumed chiasms in such a manner is pointed out by Schrader and Schrader ('26) in *Icerya*, where the two haploid chromosomes are longitudinally split and spirally twisted. There can be no question here of confusing synapsis and splitting, for there is but a single one of each chromosome present. Nevertheless, just such figures as Janssens bases his views upon appear. (See Schrader and Schrader, text fig. 6 and fig. 11, Pl. VIII.) Every appearance of the chromosomal elements is suggestive of mobility and it requires little imagination to account for all the varied chromosome forms encountered in meiosis when it is realized that the chromatids have their own inherent powers of movement. The asymmetries on the two sides of the equatorial plate in anaphase chromosomes, which were instanced prominently by

FIG. 13. COPY OF JANSSENS' ('24) PL. IX, FIGS. 179–193, TO WHICH REFERENCE IS MADE IN THIS PAPER

Attention is called particularly to the exact concordance in the structure of the cross-shaped chromosome in metaphase, fig. 183, chromosomes 6, 7, 10; and in early anaphase, fig. 186, chromosomes 2, 4, fig. 187, chromosome 2. Contrast these with oblique view of similar chromosomes, fig. 182, chromosomes 13, 21, 23. It is of interest to compare the symmetrical appearance of the ring, fig. 183, chromosome 14, with chromosomes 13, 15, 16 of the same figure.

Janssens as evidence of profound internal chromosome changes, are nothing more than indications of this individual movement on the part of the chromatids. Diagram XXIII (Janssens, '09), is illustrative of this condition and will serve as an example (fig. 12).

THE STAUROSOME THEORY OF CHODAT

Recently ('25) Chodat has come to the support of chiasmatypy by describing in *Allium ursinum* the formation of reconstituted chromosomes which he calls "staurosomes." The basic figure here is the old familiar one of two bent chromosomes twisted about each other and joining laterally near the ends. No explanation has ever been offered for the constant establishment of just such relations, with overlappings symmetrically placed at the two ends of the chromosomes, and Chodat offers none. They just happen. Upon this event the ends diverge appropriately, the chromosomes split, exchanges between homologous chromatids take place at the point of contact, symmetry is established, and a split ring takes its place on the spindle. There is nothing new here except the peculiar configuration of the crossed ends of the two chromosomes and the same criticisms apply as in the case of similar figures given by Janssens. As I have taken care to point out on several previous occasions, it is rather significant that in the representation of such crossed chromosomes no one ever gives figures showing end views of the combinations. Always it is a side view that is represented. The reason for this is obvious to one who has sought for appropriate figures, for, viewed from this aspect, ring chromosomes show perfectly symmetrical arrangements of the parts and no such lateral displacement as would be required by Chodat's assumption. Curiously enough on rare occasions there do occur instances when tetrads take their places on the spindle with homologous chromosomes superimposed. In this case an end view sometimes shows the obliquity which would be required. One figure given by Janssens ('24) suggests this condition (fig. 13, Janssens' fig. 183, chromosome 4). Such exceptional cases, however, give no warrant for the disregard of the typical, normal state of organization in the tetrad, and it does not appear that the representations of the "staurosomes" by Chodat, and of similar figures by other authors, are based upon such real appearances, but rather are due to misinterpretations of optical images.

SEILER'S CRITICISM OF CHIASMATYPY

In a recent paper Seiler ('26) reviews chiasmatypy and from general consideration of germ cell conditions reaches a conclusion adverse to that of Janssens. While I do not believe that it is possible to evaluate correctly cytological evidence in the absence of personal familiarity with the material under discussion, it must be admitted that there is a conformity to certain general principles of behavior in all germ cells, and that accordingly it is permissible to call into question any interpretation which departs widely from the one grounded upon the consistent studies of many investigators. It is perfectly evident that the basic chromosome forms upon which Janssens based his conception—the cross and ring—are common structural conditions in a wide variety of plant and animal germ cells. On the ground of such a community of conditions it seems entirely justifiable to question views that are not concordant within the range of resemblances. From this standpoint Seiler's criticisms of chiasmatypy are of value. Taken in consideration with the

fact that they are in agreement with the views of practically all other students upon the subject, they acquire additional force.

PRELL'S THEORY OF RHEGMATYPY

Because this is specifically a review of the single conception of chiasmatypy, it does not seem desirable to consider at length theories of chromosome reconstitution based upon other phenomena than chiasm formation. There may, nevertheless, be a justification in referring to Prell's "rhegmatypy" in view of the fact that it does not differ in principle from some of the later modifications of Janssens' own views. Certainly when Janssens claims that internal reconstruction of the chromosomes may take place at any period of meiosis, and when he asserts that the segregational division of one chromosome and the equational division of another in one mitosis represent the essence of chiasmatypy, then this enlarged view embraces in effect all similar explanations. Accordingly it may be stated that in putting forward his theory of rhegmatypy Prell is, in principle, supporting the position of Janssens and even in the details of the mechanism involved does not differ from certain modifications of chiasmatypy developed in its last presentation.

Rhegmatypy is represented to be a process by which, the total amount of chromatin presumably remaining constant, fragmentation increases the total number of chromosomes as between species while combinations reduce them. The result is to produce, necessarily, different groupings of genes. Such reductions in number by unions of chromosomes is not a theory but has been clearly demonstrated in the Acrididae (McClung, '17). In *Hesperotettix viridis* there may be as many as three euchromosome multiples in one individual while another has none. *Chorthippus*, *Chloealtis* and European species of *Gomphocerus* show a permanent union of the same number of chromosome pairs. Fragmentation, increasing the total number of chromosomes in cells, has been described by Hance in the somatic cells of the pig. The experimental and cytological studies on *Drosophila* have shown that genetical modifications are correlated with shifts in the position of parts of chromosomes. Metz has indicated the relation between chromosome groups in various species of Diptera and has suggested the possibilities of unions and disunions of chromosomes to account for the seriations displayed. There are numerous obvious possibilities of such physical readjustments in terms of chromosomes and, in addition, it is more than probable that specific differences in chromosome numbers may result from intimate regroupings of more elementary chromatin aggregates. Unless it can be shown that there is some determinable system in such variations, our progress is not much advanced by giving new names to old facts.

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ANIMAL AGGREGATIONS

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I. INTRODUCTION

IT HAS long been known that animals may aggregate into groups or clusters, more or less closely associated, in which physical contact may, or may not, occur. Normally actual physical contact is found as a part of the aggregation phenomenon in many Protozoa, *Paramecium* for example; in flat worms such as the planarians; in earthworms; in arthropods and molluscs; and among many vertebrates, including fish, frogs, reptiles, birds and mammals. Among other animals similarly widely distributed through the animal kingdom aggregations occur in which constant physical contact is not normal. These may be illustrated by the swarms of gnats that dance together like animated particles; by ants, bees, schools of fish, flocks of birds, herds of ungulates and groups of various other mammals, including man.

These two types of animal aggregations are not mutually exclusive, for the animals under consideration may show first one and then the other in different phases of their life or seasonal cycle. Thus honeybees, though colonial, are normally out of physical contact with their fellows; and yet during swarming and in cold winter weather, they aggregate in dense clusters in the closest possible physical contact. Ants and other animals behave similarly.

There are also abundant cases of more complete change in the reactions of animals toward each other; they may lead wholly or partially solitary lives during part of their seasonal or life cycle and come together in flocks or in actual physical contact at another period. Such is the case with the grackles, which nest under separate conditions and then join in large flocks during the migration, or with deer, which summer separately or in partial family groups and then winter in herds, or of frogs, which remain practically solitary during the year, except for possible hibernation groups, and then aggregate during the breeding season, or of land isopods, which congregate into dense bunches on the approach of certain adverse conditions.

The aggregations of the physical contact type are of necessity transitory in character in motile organisms, while in sessile animals, such as the ascidians or the marine mussels, this may well be the normal way of living. The physical contact type of aggregation finds its most complete expression among the sessile colonial organisms that grow in dense stands, consisting of many individuals physically connected with each other throughout life. Hydroids of *Obelia* represent this growth form.

The aggregations of the non-physical type, that is, the flock or the herd, may be constant and normal for some species. This is usually spoken of as the social habit. It finds its best expression in insects such as the ants and termites, among whom polymorphic forms have evolved that do not complete their sexual development, but serve the colony in other specialized capacities.

Animal aggregations may be classified

on many other bases besides that of the degree of physical contact. Deegener (45) has made an exhaustive classification of the different forms of animal groupings (*Vergesellschaftung*) in which he undertakes to arrange logically all such associations, ranging from the relatively simple colonies of *Synura* or *Charchesium*, where all the individuals are similar, all arise from the same parent cell, and all are organically connected with each other, to colonies of ants with their complicated social structure, which may include their slaves, their commensals, their tolerated guests, parasites, parasites of the parasites, etc.

Deegener's primary division is into "accidental" and "essential" societies. The distinction is made on the basis of the supposed usefulness of the grouping to part or all of its members. Unfortunately this major division is made as a result of observation and speculation only and must be revised as the field is attacked by modern experimental methods.

It is of decided interest to us to find Deegener recognizing all such groupings in the animal kingdom to be aspects of a single series of phenomena, the more highly developed of which we have been accustomed to regard as making a separate category of relationships which we have designated as social.

Deegener's first subdivision is on the basis of the composition of the group: homotypic, if it is made up of representatives of a single species; heterotypic, if representatives of more than one species are present. Then come divisions based on such criteria as whether or not the members of a colony are organically connected; whether they are grouped together from the beginning of their life or come together later; whether all or only part of the animals benefit from the association. Finally come distinctions based on the particular factors that cause the group to assemble. Thus among the "accidental" aggregations we find "Synchoria," which occupy the same place; "Synchaemadia," which over-winter together; "Sympedia," which are groups of offspring of the same mother; "Symphagia," groups that cluster about the same food, etc.

Deegener apparently would classify the animal association of modern animal ecology as a "Heterosynchorium," since it is composed of several species occupying the same place without the individuals making the group being of obvious advantage to each other. He does not recognize the existence of such an association when some of the animals are benefited.

An ordinary ant colony, considered only in regard to the ants themselves, he would class as a "heteromorphic gynopaedium," which means that it is composed of unlike individuals associated with their female parent; a termite colony becomes a "polymorphic patrogynopaedium," since both sexes are present with their polymorphic offspring. These examples will suffice to show the extent of the classification, and the expressive and correct, but cumbersome terminology proposed.

In the present paper we are primarily interested in those groupings of free living, motile animals that come into close physical contact but are not obviously and intimately integrated into a social unit. In other words our main attention will be fixed on what Deegener regards as "accidental" rather than "essential" associations, but without including sessile colonial forms. Such aggregations may be spoken of as congregations, groups, clusters, or bunches, with various shades of meaning. The term aggregations is purposely used in a large, loose sense to cover the whole range of phenomena to be discussed.

It will not be possible to extend the scope of this paper to include all phases of the aggregation reactions of spermatozoa and of swarm spores of plants, about whose activity a large literature has developed (120). They exhibit to some extent many of the phenomena to be discussed later.

II. METHOD OF FORMATION OF AGGREGATIONS

1. *Tropisms*

The method of formation of aggregations excited much attention in the three decades from about 1888 to 1918. One group of investigators, headed by J. Loeb (122) were chiefly interested in the phenomena concerned with forced movements. When exposed to certain stimuli some animals react as though they were automatons forced by the interaction between their own organization and their environment to move in certain directions and thus to aggregate when available space is limited. Such reactions were originally spoken of as tropisms and may well be illustrated by the reaction of the larvae of *Arenicola*. Mast (129), who has been consistently critical of interpreting any animal reactions as approaching automatism, says: "There is no trial reaction in this process." The movements appear little more voluntary than the precise movement of algal swarm spores. Under these circumstances the larvae aggregate automatically if space near the light is limited.

Galvanotropism frequently yields aggregations in as diagrammatic a fashion (122).

2. *Trial and error*

On the other hand animals may congregate as a result of a series of reactions which suggest the human method of "trial and error," as described by Jennings (109) or, as Holmes has put it (94) by the selection of random movements. The classic case of this sort of aggregation is that described originally by Jennings, when paramecia collect in a more acid portion of the water they occupy. This kind of reaction is so well known as to have been diagrammed by all the current textbooks of zoology. It is worth emphasizing, however, that such a method of formation of an aggregation is not necessarily less mechanistic than is the type of reaction given by the larvae of *Arenicola*. It is also of interest to us that as the paramecia aggregate, the carbonic acid given off as a result of their normal metabolic activities tends to keep the region more acid and thus to perpetuate the aggregation.

When there is a limited amount of space available, or a limited amount of optimum space, aggregations may form from either of these two reaction methods, depending in part on the nature of the stimulus emanating from the favorable locality, but in the main on the reaction system of the animals involved.

If the conditions are such that directive stimuli are absent, aggregations, if formed, will result only from the method of "trial." This apparently happens many times in nature and in the laboratory. Thus coccinellid beetles form hibernating aggregations (13) under protecting rocks and land isopods will gather (4, 7) about a small inequality of an otherwise homogeneous substratum of filter paper. Isopods readily do this when they are in darkness and probably find the inequality only by the sense of touch in random exploring movements. To animals of more highly developed nervous systems such places as the shelter of a rock or an inequality of the substratum, if perceptible at a distance, may serve as a sign of favorable conditions to which the animals would

then react (129). With animals on lower levels of nervous development, and certainly with isopods in the dark, the reaction must be a direct one to the immediate individual experience.

Such behavior as we have been discussing is obviously the result of the reactions of animals to their physical surroundings. As will be seen later, in the absence of elements usually found in the normal physical environment, animals may so react to each other as partially to substitute for the normal environment; that is, other individuals may take the place usually occupied by non-living environmental items. Three types of explanation have been advanced for this kind of phenomenon, two of which imply some innate social tendency, and another which explains such aggregations in the same terms we have already been discussing. These may be taken in order.

3. *Wallin's Prototaxis*

Wallin (203) has postulated a tropism which he believes to be of fundamental importance in the reaction of cells of multicellular animals as well as of animals in general. This tropism he designates as "prototaxis." Now a tropism may best be understood as being a reflex action of an entire organism. Animals or cells exhibiting prototaxis are supposed to have an innate tendency to react so that they form aggregations (positive prototaxis) or so to act as to remain solitary (negative prototaxis). When one examines this tropism he finds that unlike most, it is a compound affair due in part, according to Wallin's account, to chemotropic reaction. We also know that thigmotropic behavior is also frequently concerned. In fact this "tropism" becomes very much like the type of reactions usually referred to as instinctive by older writers, except that no one would have called the reaction of tissue cells instinctive.

4. *Instinct*

Deegener, both in his earlier studies (45) and in later ones (46, 51), concluded that aggregations are caused by the presence of a group, or social, instinct. Thus he comes to the same unilluminating conclusion reached by so many of his predecessors in this field.

The question immediately rises as to what social instincts may mean. Szymanski (197) undertook to investigate this problem by comparing the reactions of isolated caterpillars of *Hypnomenta* and *Arye* with those given by groups of caterpillars placed in the same general region. He believed that one can recognize reactions in the group similar to those given when the animals are alone. These he would designate as primary reactions. It follows that reactions given in the group that differ from those of isolated individuals must be due to the interaction of different individuals on each other. This he would call secondary or social behavior. This is the development of a similar idea held much earlier by Tarde (198).

5. *Aggregation by individual rather than social reactions*

Szymanski found that the factors causing the aggregations of caterpillars under experimentation were, first, the crowding of many individuals into a small space; second, tropistic reactions; third, the differential reflexes depending on whether the anterior or the posterior end is stimulated; and fourth, the method of locomotion and feeding. He thinks that groups are formed as the result of the primary individual reactions, not of the secondary social ones, at least in the cases studied. He deprecates, rightly, the tendency to emphasize social instincts as factors in colony formation when it is possible to explain the observed phe-

nomena otherwise. Krizenecky (114) came to similar conclusions.

The observations on water striders (67, 104, 164), *Notonecta* (35), *Belostoma* (181), and frogs (40), as well as the tremendous literature on general animal behavior to which reference has already been made, indicate that aggregations do form in many cases without evidence of a positive social instinct. Thus it will be unnecessary to assume a social instinct or urge in order to account for the formation of many of the animal aggregations to be discussed. The only social trait necessary in many cases is that the animals shall be willing to tolerate the close proximity of other individuals. Once formed, aggregations may remain for some time merely because of lack of disruptive stimuli.

III. GENERAL FACTORS CONDITIONING AGGREGATIONS

In many animal species the formation of aggregations depends on the physiological state of the animal (63). This may be controlled by internal developments, such as the maturing of the sex products, or by external factors, as when land isopods are made to bunch by controlling the moisture of the substratum; but more commonly the internal and external factors are closely combined. Some of the more outstanding of these conditioning factors are discussed.

1. The breeding season

a. Water isopods. My own attention was drawn to the general problem of animal aggregations while studying the factors controlling the rheotropic reaction in the common water isopod *Asellus communis*. As spring came on the stream isopods no longer gave highly regular, positive response to the water current but might strike across a strong current, guided apparently by sight, and seize another isopod, male or female. From such a beginning one might soon have all the isopods under observation gathered into a compact rounded cluster, rolling over and over in the water.

During the height of the breeding season stream isopods disregard the stimulus of a water current almost completely unless they are isolated, and even then they frequently fail to give the usual response. On the other hand, I have repeatedly tried to induce half-grown Aselli to form such a cluster, even placing them in a vessel with rounded, smooth bottom where they were continually brought in contact with each other, but no real aggregation resulted. Bunching may be induced in adults out of the breeding season, but many conditions that favor it in April during the height of the breeding season have little or no effect in late May (5).

b. Frogs. With the approach of spring, frogs desert their hibernation quarters for breeding places in the shallow ponds (40). Many hibernate in the mud at the bottom of these same ponds, but others winter elsewhere, perhaps in nearby bodies of water or on land among masses of dead vegetation or in localities similarly favorable. Cummins suggests that such frogs may migrate to open water caused by the early melting of ice in a pond with proper exposure. Banta (11) and Yerkes (216, 217) find evidence that frogs may respond to frog calls and splashings, particularly during the spring breeding season. Studies on the breeding migration of toads indicate that with them the voice serves as a sex call (36, 134).

Cummins (40) concluded as the result of his observations on a partially fenced pond that voice is not an essential inciting or guiding factor in the spring migration of frogs, since intense migrations followed periods in which there was no croaking in or near the pond, and on the other hand,

great vocal activity was not accompanied by increased migration. Certainly vocal activity cannot account for the migration of the voiceless *Ambystoma*.

The immediate inception of the migratory impulse must be intrinsic and is probably associated with the condition of the sexual glands. It is secondarily conditioned by weather, since waves of migration are coincident with high relative humidity and with a temperature of from 41 to 52 degrees F. The migration is independent of daylight. All the illuminating observations of Cummins still give no information as to why the frogs congregate in a given pond or how they learn of its existence. He does record that the migration routes are not direct, so that we may assume that we are dealing, in part at least, with random movements, probably largely controlled by temperature. Casual observations would indicate that the migration of *Ambystoma* is controlled in the same fashion.

During the breeding season a gregariousness appears among frogs which does not exist under usual circumstances. This is not entirely accounted for by the tendency which the animals exhibit to seek a similar habitat for breeding (96), for if there are only a few pairs of frogs in a given place, they force themselves together as closely as possible and the eggs form a continuous mass (72).

At the height of the breeding season several males will struggle for the possession of a single female (11). The struggles attract still other males, so that one female may become the center of a struggling mass. One such group which Banta caught had six males fastened together about a single female and five others nearby but not yet attached. The actual egg laying and fertilization of the eggs is accompanied by the formation of a close aggregation (72). In addition to the male that has been *in copulo* for some time these supernumerary males gather and, despite kicks from the first male, still manage to form a close clump. In *Rana fusca* one may find single pairs, but as a rule fertilization is a community matter. Supernumerary males also crawl over and among the egg masses and effect the fertilization of ova which may not have been reached by spermatozoa at the time of their discharge.

At the close of the breeding season, frogs scatter and resume a solitary, nonsocial existence.

c. Fish. Similar breeding clusters of fish have been described (159) with many identical details. With the rainbow darter smaller supernumerary males crowd about the spawning pair and appear also to shed spermatozoa. Reighard (160) has seen such behavior but in the main his studies (161, 162) emphasize the orderly spacing of breeding holdings in fish, a phase of the aggregation phenomenon with which the present report is not greatly concerned.

d. Snakes. Snakes are reported to form bunches in the breeding season similar to those described for frogs (53, 66, 174). Ellicott (66) records:

> I first saw such a bunch of snakes on the stony banks of the Patapsco River, heaped together on a rock and between big stones. It was a warm and sunny location where a human being could scarcely disturb them. I reasoned that the warmth and the quiet of that secluded place had brought them together. Some hundreds could be counted, and all in a very lively state of humor, hissing at me with threatening glances and with such persistency that stones thrown at them could not stop them nor alter the position of a single animal. They would make the proper movements and the stone would roll off; all the snakes in this lump were common garter snakes (*Eutaemia sirtalis* L.).
>
> The second time I noticed a ball of black snakes rolling slowly down a steep hillside on the bank of the

same river. Some of the snakes were of considerable length and thickness and, as I noticed clearly, kept together by procreative impulses.

e. Lunar periodicities. Such breeding aggregations are much more important in fresh water and land forms, with whom the surroundings are more injurious to shed sperm and eggs but they do occur among marine animals. With marine organisms the most spectacular expression of breeding aggregations is to be found in the case of the large number of animals whose breeding rhythms coincide to some extent with lunar periodicities. The literature on this subject (75, 83, 108, 112, 119, 121, 131, 143, 215) is extensive and while the facts are plain enough the fundamental causal relationships remain unknown. One illustration must suffice, based on the account given by Just for the swarming of the sea worm *Nereis limbata* in the waters around Woods Hole (112).

Nereis limbata has its swarming period only after twilight. Each run begins near the time of the full moon, increases to a maximum during successive nights and sinks to a low point about the time of the third quarter, again rising and falling to extinction shortly after the new moon. They appear in four periods or cycles during the summer, corresponding to the lunar cycles in the months of June, July, August and September.

Only fully mature animals swarm. The swarming begins shortly after twilight and lasts only for an hour or so. The swarming animals are attracted by the light of a lantern. Males appear first, darting through the water in curved paths in and out of the circle of the light. Females are fewer in number and swim more slowly. The males outnumber the females hundreds to dozens. In the next few minutes the numbers increase, waning again after about three quarters of an hour.

New females appear each night, but some males may presumably reappear on several successive nights. A swarming female is soon surrounded by several males. These swim rapidly in narrow circles about her. In a little while they begin to shed sperm, probably in reaction to some secretion from the female, rendering the water milky. Soon the female begins to shed her eggs, shrinking in bulk as she does so, until, a shadow of her former self, she sinks through the water to die.

2. *Hibernation*

Overwintering aggregations of animals have long been known. This phenomenon with social bees has been noted in scientific literature for almost two centuries (158). Barkow (13) in his monograph on hibernation written over three-quarters of a century ago has a short chapter in which he calls attention to the winter aggregations of lepidopterous larvae, adult ants, bees, true bugs, beetles, including the frequently observed case of the coccinellid beetles, carp and eel-like *Muraena anguilla*, snakes, frogs, and a few mammals, including marmots and bats. Barkow advances no theory to account for the congregation of these animals, but states that there is a suggestion current that the animals aggregate as a result of response to their sense of smell.

This list of overwintering aggregations has since been much extended, especially by Holmquist (98, 99), who has made extensive studies on hibernating arthropods in the Chicago region. He reports that of 329 identified species taken during the winter season nearly 17 per cent were more or less closely aggregated. Omitting those known to be of somewhat social habits at other times of the year, about nine per cent of the species ordinarily solitary in the summer were aggregated in winter.

In the social bees careful experiments have shown that temperature control results from such clusters (153, 154) and Holmquist has unpublished data showing that other benefits may accrue from the cluster formation of hibernating ants.

In many cases these overwintering groups are essentially shelter aggregations apparently due to the small amount of serviceable shelter available. Often, however, not all the apparently equally desirable space is occupied, so that the aggregation cannot be entirely explained on the basis of unavoidable crowding. In other cases Holmquist has been unable to find any environmental differences to account for the location of the hibernating aggregation. These groupings are partially under temperature control, but as with other phenomena connected with hibernation, the temperature control is incomplete and the problem of the exact nature of the causal factors remains open.

3. *Aestivation*

Aestivating aggregations have been less studied. Land isopods will form aestivating groups which may be either homotypic or heterotypic. They have been reported to collect in large numbers in protected places and so pass the long, hot, dry summer of southern California (1).

4. *Moisture control*

The chief controls of the aestivation reaction of these isopods are temperature and moisture. Of the two, laboratory experiments show the latter to be more important (7). When land isopods of various species are placed on air-dry filter paper they collect in bunches within a few minutes unless the substratum is too dry. In this case they will run about actively until at the point of death. If the substratum be moist, the same isopods will remain quietly scattered. A somewhat similar effect of drought in nature is reported for the California quail (68). In an unusually dry season these quail do not breed but remain in flocks during the entire summer. The opposite type of moisture control is also observable. Too much moisture may induce well defined aggregations. Thus *Solenopsis geminata* (202), a species of ant which often nests in lowlands will, if the nest is flooded, aggregate in a ball of some 15 to 25 cm. in diameter with the larvae and pupae inside. By constant rotation they avoid too long submergence and at length may come against some solid object and so escape from the water. Wheeler (205) cites this case and mentions similar instances in this and other species of ants.

The formation of the dancing bunches of midges that one frequently sees aggregated in the space of a half bushel basket appear to be in part conditioned by the atmospheric humidity, although the absence of wind is another obvious prerequisite.

In both these cases the environmental conditions are uniform and the animals in grouping together react to each other only. There are also the place aggregations controlled by moisture when animals will collect in a limited area because it provides an oasis of moisture in an otherwise overdry environment. Thus land isopods can be made to collect at will in a given spot by making it moist. Selous (178) gives a striking picture of the congregating of large ungulates about an African drinking hole in the dry season. The common fruit fly, *Drosophila*, shows a somewhat intermediate condition when, struggling to escape too great moisture, it aggregates in shifting masses at the top of a projection; these masses continually fall apart and re-form as the flies move up again. When transferred to a dry bottle they resume normal behavior and spread over all the interior surfaces.

5. *Lack of normal environment*

The snake starfish, *Ophioderma*, lives in eel grass in certain locations along our eastern coast. Repeated efforts in summer months have failed to reveal this animal in contact with others of its kind in nature. They are often found near together but never aggregated.

Ten of these starfish were introduced into a laboratory aquarium made to approach normal living conditions by the introduction of eel grass. Nineteen hours later seven of the ten animals were sighted after a search lasting half an hour. One was found on the bottom at the side away from the strongest light; six were in the densest part of the vegetation in the same region, and although not in immediate contact, all of them could probably have been enclosed in a five-inch cube. The exact location of the other three could not be observed without disturbing them. Animals in the field are probably also close together without actually touching. Only such loose collections were ever seen in this eel grass aquarium. Extended experience with these animals in the laboratory leads me to conclude that the tendency to bunch is greatly reduced in proportion as favorable natural conditions are approximated, and that the animals so congregated are usually found in regions to which they have been directed by their tropistic reactions.

When, however, *Ophioderma* are placed as they are collected in a glass or similar container, they form dense mats of bunched animals with arms closely interwoven. The aggregations form in the shadiest part of the dish and are to be explained in part by the fact that the lower animals are shaded by the upper ones and so, having satisfied a negative phototropism and a positive thigmotropism, they remain quiet.

When these starfish are isolated and left for a week or more in separate dishes exposed to light frequently the arms are moved into contact until they present a sort of self-bunching.

Laboratory aggregations occur in a large number of animals. May-fly nymphs, various isopods, earthworms, frogs, etc., may readily be observed to form such bunches. The reaction appears similar to that which causes the collection of foreigners into communities in our large cities; that is, a group of similar animals tend to minimize for each other the disturbing effects of unusual surroundings.

6. *Sleep*

Fabre (69) found some hundreds of *Ammophila* (*Sphex*) *hirsuta* assembled under the shelter of a stone on the mountain side and speculated much concerning this gregarious condition of a solitary wasp. The Raus (156) found three related species sleeping in such assemblies, from which it would seem probable that Fabre was observing a slumber aggregation. With *Chalybion caeruleum* both males and females may be found aggregated at night in about equal proportions. As many as a thousand have been found in one colony. Marked individuals will return to the same sleeping place for at least two weeks. No one knows how the male of the species passes the day; the female labors about the nest in the daytime.

The solitary *Sphex* wasps appear to choose their sleeping quarters independently, but since they select the same sort of place, they tend to form spaced aggregations. *Prionyx* sleeps sometimes singly, sometimes gregariously, crowded close together on the top of a weed with equal numbers of males and females present but without observed copulation. The males and females of the horse fly, *Tabanus sulcifrons*, are reported also to collect

(90) in favorable places to sleep. Similar observations are on record for various other insects.

There is no evident protection from enemies in such assemblies. The sleep may be sound and extend so late that early birds could pick off the sleeping insects in numbers, as beetles are reported to kill sleeping butterflies (73).

The congregation of birds for sleeping has been widely observed (14, 25, 44, 208) particularly for martins, robins, grackles and crows. Many other birds are reported to gather in the roosts dominated by martins and robins. It is well known that bats also gather into sleeping aggregations (8, 82, 102). They may congregate in clusters comprising only a few individuals, or hundreds may hang with bodies touching. Some cluster so only in the daytime, others only at night. The groups may be homotypic or heterotypic. To the human senses these bird and bat roosts are easily detected by their odor, and perhaps that is a factor in guiding the bats to the sleeping place.

Allen (8) has banded clusters of these bats. He records recovering three of a group of four from the same place where they were banded after an interval of three years.

These sleeping aggregations appear to be without mating significance. The Raus did not see copulation among the insects they observed; in fact, in many cases, the sleeping groups were composed of males only. The robin roosts may contain both sexes and all ages of birds above the nestlings. With crows the common roost ends with the beginning of the breeding season, except for the bachelors, and in general these roosts are not occupied by the breeding birds. After the breeding season the birds may return in family groups, a situation to be discussed later at more length. In the bats the sexes are segregated (102) during the time of gestation and of the care of the young.

IV. HOMOTYPIC VS. HETEROTYPIC AGGREGATIONS

Heterotypic aggregations are those which are composed of more than one species; they appear to be of common and widely distributed occurrence. Unusual and dramatic combinations are frequently recorded, as that of fox and caribou (52, 190), fox and mountain sheep (182), predaceous and non-predaceous insects overwintering in the same restricted hibernaculum (98) and mixed herds of the large African animals, to which reference has already been made (178). The phenomenon of mixed flocks is well known among birds. The most extraordinary that has come to my attention is that recorded by Beebe (15) who observed a flock of 28 birds composed of 23 different species. Such heterotypic aggregations closely approach the associations of the ecologists.

The interesting problems with heterotypic aggregations concern the relative ease with which they may be formed and the degree to which they may become integrated as compared to homotypic groups. Land isopods form such groups and preliminary studies have not shown essential differences so far as physiological effects are concerned. There is evidence with the isopods, however, that heterotypic groupings occur more slowly than do the homotypic ones. Young spiders of the genus *Epeira* will mingle if family groups are intermixed (46), forming associations which are apparently as firm as if composed of but one family group; but different species of the same genus will separate out peaceably into distinct groups even if well mixed. In ants, of course, the antagonism may be much stronger; but

the situation in such social animals does not come within the scope of this review.

V. RESULTS OF AGGREGATIONS

After all we are less concerned about the methods of formation of aggregations and the factors conditioning them than we are with the physiological effects which such aggregations produce upon the individuals of which they are composed. The type and extent of such effect makes one of the crucial tests of the importance of the phenomena. If these aggregations are merely forced reactions resulting from limited space or from blind tropistic behavior or if they result only as an expression of a social instinct, their significance is much less than if they can be shown to have group value. Failure to observe such values for many aggregations led Deegener to conclude that their formation must be due to some inexplicable instinct.

In other words, in the investigation of this problem we must first inquire whether or not the aggregations have survival value. If such be found in a number of cases the problem is by no means solved, but the methods to be used in its solution will be more clearly indicated.

A. Harmful effects of aggregation

From the older, grosser point of view dominated by the idea of a struggle for existence between animals such aggregations are more obviously harmful than helpful, at least until they become sufficiently integrated so that members may be warned of the approach of danger by the multiplicity of eyes in the group, or can attack or defend more advantageously as a group than as single individuals.

An aggregation of *Dermestes* beetles feeding on a limited amount of carrion exhaust their food sooner when the group is larger. This aspect holds true whether we are concerned with leaf-eating caterpillars, sap-sucking aphids, or tissue-filling parasites. It is only with predators catching lively creatures as food that the feeding aggregation becomes of value. A school of young catfish is much more likely to catch a given *Daphnia* than is a single individual, and each member of the group is more likely to feed upon the *Daphnia* stirred up than if he swam alone.

The same number of individuals are obviously more easily gobbled up by an enemy when aggregated than when scattered. One of the sleeping clubs of bees or wasps described by the Raus would provide a substantial breakfast for the proverbial early bird, and a hungry centipede would have easy picking in a group of aestivating land isopods. Similarly a bunch of starfish in a limited amount of water exhaust the available oxygen more rapidly than would a single individual.

1. Deleterious effects of crowding

Jabez Hogg (92) apologized to the London Microscopical Society in 1854 for taking up their time with some observations on the pond snail "*Limneus stagnalis*" which had already been the subject of microscopical examination by such masters as Swammerdam and Réaumur. Then in the midst of his other painstaking observations he records that a snail kept in "a small narrow cell will grow only to such a size as will enable it to move freely" and this is the first recorded observation of the limiting effect of volume on growth.

Twenty years later Semper (179, 180) extended this observation to include the dwarfing effects of the presence of several animals in a limited space as compared with a single individual in the same amount of space as that occupied by the whole group. The whole literature on this point is much too extensive to review

or even to list here. Colton (37) writing about twenty years ago gives a good summary of the early literature and adds his own confirming evidence.

The dwarfing effect of crowding has been widely observed in the animal kingdom and has been found to affect both growth and reproduction. Recently Bilski (16) studied populations of tadpoles and derived a fairly simple mathematical formula to describe the influence of the density of animals upon the rate of growth. Pearl (145) and his associates have found that a similar equation describes the effect of density in cultures of *Drosophila* upon the rate of reproduction. Pearl points out that both equations closely resemble that of Farr for describing the relation between death rate and the population density in human communities.

A large number of suggestions have been put forward to account for these crowding effects. Hogg in 1854 said naïvely enough that the animals adapt themselves to the necessities of their existence. Semper, twenty years later, unsatisfied with this statement but unable to find any specific causal agency, postulated the presence of some unknown substance necessary for growth as oil is for machinery. This material he thought must be absorbed in a definite quantity if growth is to be normal. Since the substance was supposed to be present in minute amounts, the greater the crowding in a given volume, the less the growth. Pearl writing only last year concerning the decreased egg laying in the crowded chickens could not be much more definite. He postulates an unexplored physiological disturbance which "in our ignorance we must call psychological."

Fortunately some progress has been made with water animals towards finding the causes of this physiological disturbance. Semper cites the obvious limitation of food as one cause. Yung (218, 219) found that lack of oxygen causes dwarfing of tadpoles. Vernon (201) concluded that the echinoderm larvae he studied in restricted volume were stunted by the increased concentration of excretory products. These observations have been widely extended. The limiting effect of excretion is particularly marked in ciliate infusions (84, 212, 214). Recently Goetsch (81) has introduced a clever experimental method which allows him to separate the factors of available space from available volume. He introduces into his experimental aquaria, tubes thrust through corks to keep them afloat. The lower end of the tube is covered by gauze, which allows diffusion connection with the whole aquarium but limits the amount of available space. By equalized feeding another obvious factor is controlled.

Goetsch experimented upon sessile hydra, slowly moving planaria, and amphibian larvae which are capable of rapid locomotion. As might be expected he finds different factors important for different animals. Thus with hydra, volume per animal is the controlling factor because of the restriction of food which it conditions. There is no stimulation or depression caused by the crowding of hydra in a narrow space and within reasonable limits concentration of excretory products is not effective. With planaria food is again the most important factor but growth is markedly inhibited by the concentration of excretion products or of stale food. With the active amphibian larvae, if food is controlled, the major limiting factor is furnished by the more frequent collisions in a dense population or in restricted area with the concentration of excretory products playing a wholly secondary rôle.

Drzewina and Bohn, in connection with their studies on the relation existing between mass of toxic liquids and the contained mass of animals have found many cases of protection furnished by increasing the numbers of animals present in the same

amount of solution. These will be reported later. In some instances they record the opposite results (58, 59).

When KCl was used as a toxic agent with cultures of *Convoluta*, a small marine planarian, other things being equal those in the solution containing the larger number died first. Similar relations hold when the same number of individuals are placed in differing amounts of the same strength of KCl solution. Those in the smaller amount of liquid die more rapidly. The freshwater planarian, *Polycelis nigra*, reacts similarly. These investigators believe that the planarians give off a substance which causes auto-destruction, and obviously, if this be true, such destruction is hastened by increasing the mass of individuals in proportion to the amount of liquid.

Their interpretation is supported by the observation that if two fresh planaria are introduced into a solution of KCl which has already contained others, their death is hastened, but if, after an hour in such solution one removes them to a new solution of similar strength, their death is again retarded. Before accepting this hypothesis it would be desirable to inquire into the oxygen tension and respiratory exchange under the various conditions. Some of the relations outlined are those which one would expect from decreased oxygen tension.

As these selected observations show, it is easy to demonstrate harmful effects from crowding of paramecia or of men. This makes the attempt to locate a positive survival value of relatively unintegrated aggregations, which the widespread occurrence of the bunching habit would lead one to expect, at once more difficult and more important.

B. Beneficial effects of aggregation

In the case of breeding aggregations and of young associated with and watched over by the parents, or of groups protected by sentinels, the gregarious habit has obvious advantages. More refined laboratory observations have revealed unsuspected benefits that may result from aggregations even in a very low state of group integration.

1. Maintenance of water content

Aggregations of land isopods will take up water less rapidly from an over-moist environment (7) than will their isolated fellows, and conversely, they will also lose water more slowly under dry conditions. The formation of bunches helps make these isopods more independent of the water content of their surroundings and markedly decreases the rate of change of body moisture when this is out of equilibrium with their environment. In this way the length of life may be increased especially when the animals are exposed to a drying environment to which they are particularly susceptible. In one experiment ten grouped isopods on a dry background of filter paper were all alive and active after 7.5 hours, when six entirely similar animals isolated under similar conditions were all dead from loss of water. Such relations are known to hold for earthworms. Shelford (184) found that a ground beetle, *Pterostichus adoyus*, may react to a gradient of different rates of evaporation either by coming to rest in the moister region or by aggregating in the driest part. The phenomenon is probably of widespread and general significance.

2. Tonus maintenance

Respiration studies on the effect of aggregation on land isopods have shown that bunched animals are respiring at a more rapid rate after the animals have stood for some time. Since the experiment was carried on in the absence of food, the rate of respiration decreased markedly in

both isolated and aggregated individuals but under the conditions tested this reduction takes place approximately twice as rapidly with isolated as with bunched isopods.

Studies of the total amount of oxygen consumed during such a starvation period by isolated and bunched starfishes (*Ophioderma*) show that the bunched individuals consume more oxygen over such a period than do the isolated individuals. Mr. M. W. Eddy, working at my suggestion, has found that aggregated young catfish (*Amieurus*) have a higher rate of respiration than do artificially or self isolated ones of the same age. Preliminary determinations on a number of other animals indicate that such conditions are widespread when the animals are tested under conditions approaching those obtaining in nature.

3. Heat conservation and regulation

It is difficult to hold to the intention of avoiding discussion of aggregations among the social animals. The matter of heat conservation by aggregating is best illustrated by the example of the honey-bees. These poikilothermal animals show some ability in regulating their temperature as individuals (155) but still more in the winter clusters (79, 153, 154). When a bee colony is without brood, if the bees do not fly and are not disturbed they generate practically no heat until the coolest point among the bees reaches a temperature of 14 deg. C. At higher temperatures the bees remain scattered over the comb. When this critical temperature is reached they form a winter cluster and begin to generate heat.

The temperatures within the cluster do not remain constant and are affected by the length of confinement and by the presence of brood, both of which cause an increase in temperature. Heat for warming the colony is produced by muscular activity within the cluster. The same fanning movements that serve to cool the hive in summer also serve, with other muscular activity, to warm the winter cluster. In winter the bees also retain water in their bodies and so avoid the loss of heat that would be necessary to evaporate it (144). Steiner (196) has described similar relations for one of the ants. He emphasizes this matter of warmth as an important factor in the development of social life in animals and maintains that animals cannot co-operate well unless they are able to remain warm over long periods of time.

4. Protection from various adverse conditions

The common brittle starfish at Woods Hole, *Ophioderma brevispina*, if isolated into glass dishes of sea water will undergo fragmentation of the arms much more rapidly than occurs when a group of ten or so are placed under wholly similar conditions. The group immediately forms a close aggregation which for some reason inhibits the animals from self-mutilation. In one case the ratio of broken arms was nearly twice as high in isolated individuals as with those grouped. Evidently the self-bunching which is frequently practised by solitary animals has not the protective value of group bunching.

a. Relation of mass of animals

Drzewina and Bohn (55) became interested in the possible protection from toxic substances furnished by a mass of animals as compared with that of a single individual exposed to the same intensity of the toxic agent. They recognized that added immunity due to some sort of group protection might explain the fact that many animals live near together in nature. Thus *Convoluta*, the tiny, green flatworm common on the coasts of Brittany, is

found in loose groups in the sands of tidal flats where they are exposed to marked dilution of the sea water by rains, particularly if the rains come at low tide. Experiments showed that these worms can resist dilution of the sea water much better when they are present in large numbers than when there are but few present.

Similarly, if placed in dilute suspensions of colloidal silver, *Convoluta* in small numbers die in about four hours, while with twenty-five to fifty times the number of worms in the same amount of the same strength of silver suspension, death occurs in about forty-eight hours. Similar relations hold over a wide range of dosage. Schuett (176) has verified this general situation, using *Planaria dorotocephala* in this laboratory.

Similar results were obtained with infusorians such as *Stylonichia*, *Paramecium*, *Colpoda*, *Vorticella*, and *Stentor* (57). In suspensions of colloidal silver of from one to five drops per cc. the resistance of tens was compared with that of hundreds or thousands. Always, when a minimum amount of the parent culture solution was introduced, the isolated individuals were much less resistant.

Drzewina and Bohn obtained similar results with tadpoles of the brown frog, *Rana fusca*, and even when different concentrations of spermatozoa of sea urchins (*Strongylocentrotus*) were treated with different toxic agents (60, 61). The sperm retained fertilizing power longer when the concentration was greater. Hinrichs (91) has found that the rate of loss of fertilizing power by spermatozoa of *Arbacia* treated with ultra violet radiation is directly proportional to the dilution.

Supporting evidence from a separate source comes from the observations of Robertson (165) upon the Australian infusorian, *Enchelys farcimen*. A temperature of 30 deg. C. prevents subcultures of this protozoan from multiplying and the isolated individual almost always dies. But shade temperatures of 30 deg. C. are known in South Australia where wild *Enchelys* live. Isolated wild infusorians brought into the laboratory gave the same reaction, but if the culture slides were populated by twenty to thirty individuals they could successfully resist exposure to temperatures of 33–34 deg. C. for as long as seven days in succession without apparent injury or abnormality. A similar number of individuals put into fresh hay infusion at this temperature survives and multiplies while isolated individuals inevitably perish.

b. Relation of volume of liquid

The converse experiment is made by keeping the number of animals constant and varying the mass of the liquid. Such experiments were performed by Drzewina and Bohn (57) with results which support their conclusions reported above. Experiments with infusorians and with a small leech, *Glossiphonia bioculata*, strongly indicate that with the solutions used the dilution of the toxic substance is less important than is the mass of the liquid environment.

The same problem in less severe form is to be met in isolation cultures of microorganisms and of tissue cells. Wildiers (210) found a relation between volume and the success of his cultures of yeast, with cultures growing better in the smaller volumes. Kuster (115) records that the isolation of a single organism in too large a volume of culture media results in death or in great delay in multiplication. Barber and associates (204) could not obtain growth from a single tubercle bacillus or an anthrax spore introduced into a guinea pig or a mouse; several must be introduced before they thrive.

Jennings (110) summarizes the experi-

ence of workers with isolated paramecia when he states that

> long continued cultivation on slides does produce a depressed condition. There are some stocks that will not stand it at all, though they live perfectly in mass culture.

It is also true when the same culture medium is used with both, that the stocks cultivated in isolated condition frequently die out while the same stock will live in mass culture.

Peters (152) lays stress on the relation between the volume of the medium and the number of colpidia growing in it at early stages in the isolation. Many attempts were made to get individuals to grow in small test tubes with about one cc. of culture fluid, but all were failures. He suggests that in order for growth to proceed, the organism has to modify its environment, probably by adding some synthesized substance in sufficient concentration for growth. When a sterile subculture containing 20 to 40 organisms has been obtained the subsequent subcultures are easily made.

Robertson (169) reports similar experiences with *Enchelys*. In his cultures, single infusoria isolated in volumes exceeding 1 cc. rarely survive and those in more than 0.1 cc. frequently fail to divide.

The tissue-culture workers have also contributed some evidence on this point. Testimony is unanimous that isolated single tissue cells do not multiply. Rous and Jones (172) were impressed, as several had been before them (173, 211), with the striking tendency to reunite that is shown by isolated tissue cells, but they did not see division or multiplication of such cells. Burrows and associates (31) state that isolated tissue cells planted in plasma may show movement but they do not grow. They find that growth takes place only about fragments of tissue, and that if the transplant is not too large, growth *in vitro* is directly proportional to the size of the fragment.

Fischer (71) found no evidence of cell division among isolated cells although he studied hundreds of such isolated fibroblasts. When ordinary tissue cultures were cut in two and transferred to a new medium the cells grew more rapidly at the center than at the periphery. If the periphery of a mass of such cells growing *in vitro* is isolated from the main body by an incision the peripheral cells no longer grow, on reincubation, although the densest part of the main cluster grows rapidly nearby.

Gemmil (80) a quarter of a century ago reported that dilution shortens the period of vitality of spermatozoa. Lillie (120) gives directions for a practically quantitative experiment testing the effect of dilution on the sperm of *Arbacia*. Extremely dilute sperm suspensions (1–240,000 per cent) lose the fertilizing power in about six minutes, while a concentrated suspension of one per cent may retain this power for more than two days.

c. Explanation of mass relations

Drzewina and Bohn present evidence that the greater immunity of the larger group is not due to the using up of the active toxic substance more rapidly by the larger number of animals. A number of infusoria in a suspension of colloidal silver of the same volume but five times the strength of another suspension will remain alive after isolated animals in the weaker suspension are cytolyzed. The relative color of the two show that more silver is still present in the medium containing the group.

The following procedure gives further evidence that the greater immunity furnished by the group is not due to the exhaustion of the toxic agent (57): Decant

off the silver colloid suspension in which fifty larvae of *Rana fusca* have stood for twenty-four hours. The color will show that silver is still present. Now add the same number of drops of silver colloid originally used and introduce two new tadpoles. As a control place two similar tadpoles in a fresh suspension of the original strength. Drzewina and Bohn report that the latter die, as is the rule for isolated tadpoles, while the former, isolated into a stronger suspension in which tadpoles have lived for a day, will survive.

From such observations they conclude that when attacked by toxic agents, animals give off rapidly a substance or substances which are protective. If the individuals are present in sufficient numbers in proportion to the volume of the reagent, the defense may be effective; if isolated it is much more likely to be ineffective. Evidently a reserve of this hypothetical protective substance is accumulated (56) until it will protect isolated individuals introduced into a decanted and reinforced solution. Less protection is furnished by water in which worms have stood, but which lacked the toxic agent, and when the colloidal suspension is diluted the protection is greatly weakened. Drzewina and Bohn have examined the nature of this protective substance and report that it appears to be specific, but the experience of this laboratory (176) has been that under controlled conditions planarians are protected from the action of colloidal silver by the presence of numbers of carefully washed individuals of *Dendrocoelum*, *Daphnia*, *Asellus*, pond snails, pond leeches, and even by pond mosses. This protection has been reciprocal whenever tested. In our experience the protective secretion appears to be the slime which many of these organisms produce in large amount and which adsorbs the toxic silver particles. Our experience in this matter resembles that of Bresslau (24) rather than that of Drzewina and Bohn.

Burrows and Suzuki (32) think that disintegrating tissue-culture cells supply nutrients necessary for growth. Fischer (71) concludes that beside the growth-promoting factors found in the tissue juices, there may possibly be something produced in the body of the cell or of certain cells only, that initiates cell division and is carried directly from one living cell to another.

Robertson infers that some necessary substance passes from the infusoria into the medium. If the amount of the medium is too great reproduction and even maintenance become impossible. He suggests that the death of isolated infusoria at high temperatures is due to the excessive loss of this substance from the nucleus on account of the increased permeability of the nuclear membrane. The group is able to protect itself because the concentration of this hypothetical substance is supposed to come to equilibrium before the individuals of the group have lost an excessive amount.

Suggestions similar to these have been made (80, 91, 120) to account for the rapid loss of fertilization power by dilute suspensions of spermatozoa.

5. The lag phenomenon

When a single cell is isolated into a new culture medium a longer or shorter latent period usually follows before reproduction begins. This is known as the lag period. It has been much studied in bacterial cultures (147), in *in vitro* cultures of vertebrate tissue and in protozoan cultures (165, 169). The duration of the lag period depends in part on the condition of the parent culture. If this is reproducing at maximum rate and if the nutrient medium is taken from that of the original culture, frequently no lag ensues (147).

With some media even under these conditions the lag phenomenon persists. Robertson (169) finds that, other things being equal, with infusorians the lag may be shortened by making a gradual transfer from the parent culture to the new subculture.

This lag phenomenon is of interest in our problem because of the indication it gives that organisms isolated into new conditions are markedly affected by the change and because of observations (147) that if the inoculum be small further diminution of the seeding lengthens the lag period; the smaller the seeding the more marked the lengthening.

Robertson's explanation of the phenomenon, although expressed in terms of his hypothesis of an autocatalytic agent, is in general similar to the older idea of Penfield's for bacterial cultures. Penfield proposes to explain the lag by assuming that some substance "*c*" may be required which is produced not from "*a*" already in the solution but from "*b*" which must be produced by the organism from "*a*."

6. Robertson's allelocatalytic effect

Robertson (171) found that when two infusorians (*Enchelys*, *Paramecium* or *Colpidium*) are freed from parent culture media by washing, and are introduced into some restricted volume of fresh culture medium, the early rate of reproduction after the lag period is not merely double that of a single infusorian of the same species similarly treated, but reaches some multiple in excess of this. He reports that he has obtained a rate of from 2.5 to 10 times that which might have been expected. This increased rate of reproduction, which Robertson calls the allelocatalytic effect, he attributes to the diffusion of some agent from the organisms into the culture medium, by which their reproduction rate is accelerated.

Fischer's work, mentioned above, in which he found that fibroblasts grow only when tissue cells are numerous and close together, can be interpreted as giving supporting evidence to the allelocatalytic hypothesis. Burrows (30), growing cancer cells *in vitro*, found a similar stimulation.

On the other hand Cutler and Crump (41) with cultures of *Colpidium*, failed to find the allelocatalytic effect if the volume of the medium is reduced, and Greenleaf (84) records his failure to confirm Robertson's work, using *Paramecium* and *Pleurotricha*. Peskett (148, 149) observed such stimulation to division in only three cultures of yeast out of 128 examined, and later in extended observations failed to find evidence of Robertson's allelocatalysis.

Robertson (170, 171) has reexamined the problem in the light of these results and explains the failure of other workers as being principally due to lack of washing the organisms before transfer. He reports the allelocatalysis increases with progressive removal of preformed catalyst until a maximal effect is reached just before its total removal. He also emphasizes an earlier statement that in comparing the reproductive rate, care must be taken to estimate the population some time before it has attained maximum density. The end result of introducing a second individual is to reduce the rate of reproduction, since the final maximum is the same in all cases and is independent of the size of the seeding.

Peskett returns to the problem in his 1925 papers (150, 151), apparently using very careful technique, washing his transplants and plotting a growth curve based on a number of examinations at different phases of the culture, but again fails to find evidence for the allelocatalytic effect.

Cutler and Crump (42) also repeated

their experiments with *Colpidium*, thoroughly washing their animals before transfer. They again failed to obtain evidence of the stimulation demanded by Robertson's hypothesis. It may be that their technique differs from Robertson's sufficiently to account for some difference in results, since the infusorians which Robertson washed were frequently injured in the process, while Cutler and Crump found no deleterious effect from their washings; or there may be a difference inherent in the stocks used.

Here the matter of allelocatalysis, of obvious interest to any student of animal aggregations, rests at the present time in a sufficiently muddled condition to merit the experimental attention it is receiving at this and doubtless other laboratories.

7. *Other evidence*

On the other hand there is a mass of evidence that organisms do produce substances capable of causing growth stimulation. The existence of vitamines (62), the discovery that organic substances extracted from bacterized peat markedly stimulate plant growth (20–23) and that preparations from a variety of living tissues yield an extract that stimulates the growth of yeast (64, 65, 77) all indicate that organisms may give off substances into the surrounding medium which might markedly affect other animals nearby.

The possibility of a more subtle effect is indicated by the work of Gurwitsch and his associates (85–87, 157), who report that they can stimulate the number of mitoses by bringing the tip of one growing onion root in close contact with another but at right angles. The effect seems to be propagated in a straight line as a pencil of radiation, which tests indicate has a wave length of about 2000 Angstrom units. They report similar results with macerated living onion tissues, but narcotized tissues fail to be effective. They even find evidence of marked heterotypic stimulation with *Helianthus* roots acting on onion, and whole or macerated rapidly growing tissue of tadpoles is said to cause some stimulation of mitoses when given an opportunity properly to radiate growing onion root tips. Obviously such effects need verification before their implications are discussed seriously.

Taken as a whole, the evidence collected independently by a number of workers upon a wide range of organisms indicates that in many cases the group may possess valid survival values. These may be much more refined than the more obvious advantages postulated by the earlier view of the struggle for existence and may easily be concealed by gross experimental methods. In fact, the obvious advantages may be lacking and still the aggregation can show survival value. Such advantages as do exist are not universal either among different kinds of organisms or with the same individuals in different environments; but the fact that they may exist even in groups brought together artificially by a laboratory experimenter indicates that they deserve serious consideration from the student of social origins.

8. *Influence of aggregations on sex*

There is another growing lot of evidence that aggregations of animals may exert a profound influence upon each other to be found in the effect of such groupings upon so fundamental a characteristic of animals as their sex. Over ten years ago Baltzer (10) found that if the young, free swimming, sexually indifferent larva of the marine worm *Bonellia* attaches itself to a female of the same species it receives a sex determining substance from the host and becomes a male. If, on the other hand, it

develops solitarily, it becomes a female. In this case organic attachment is concerned, a situation which we are not discussing seriously in this paper.

The conditions are different in the boat-shell snail, *Crepidula plana*, which is common on our New England coast. These too are protandric hermaphrodites. They live sedentary lives on the shells occupied by hermit crabs. Gould (82a) found that the development of the male phase depends on the nearby presence of a larger individual of the same species. Such an individual is frequently a female but that is not necessary, for a larger male will have the same influence. Some sort of stimulus passes from one to the other but Gould was not able to discover the nature of this stimulus. When a male becomes removed from the neighborhood of a larger *Crepidula*, the male organs degenerate and after a period of sexual inactivity, female sexual organs develop.

The relations between aggregating individuals and sex are just as interesting in the water fleas commonly called *Cladocera*. These animals reproduce parthenogenetically for a longer or shorter period during which the population is wholly female. Such a period is followed typically by an epidemic of bisexuality, the exact causes of which have long been a challenge to experimental zoologists.

Banta and Brown (12) have recently found that a crowding of the mothers will cause the production of a variable number of males, while females of the same brood, given identical treatment but uncrowded, produce only females. Dr. Agar has told me personally that he has confirmed this observation "to the hilt." Banta and Brown suggest that the appearance of the males in a crowded culture is due to an excess accumulation of excretory products, since they find that a number of depressing conditions such as lowered temperature, increased carbon dioxide tension or the introduction of uric acid has the same effect, particularly in crowded dishes. They think that the metabolism of the mothers is reduced by the effects of the crowding and that such reduced metabolic rate during the maturation of the eggs favors the production of males.

VI. AGGREGATION INTEGRATION

Animals living in a given habitat can be shown to be more or less closely interrelated. Darwin's famous demonstration in logic, proving a relation between the number of maiden ladies and the yield of clover seed in the English rural districts, is an illustration of this fact. Ecologists have attempted to systematize this "web of life" under the name of "biotic communities" or "associations" and have made it the basis for the modern development of ecology. Bodies of fresh water furnish the most complete illustration of this point of view, as was clearly pointed out by Forbes (74) almost forty years ago. In his essay on the "Lake as a Microcosm" Forbes shows the intimate relationship between all inhabitants of a small lake, plants as well as animals. The microscopic protozoa are seen to be members of the loosely integrated community as truly as the black bass, which are at the apex of the food series. Relationships concerned with food and space form the main integrating factors of such a microcosm, and these are sufficiently strong so that the whole may be recognized and treated as a unit. It is upon such units that modern ecology is built.

Obviously such a unit may be somewhat vaguely defined. As Mathews (130) says of the protein molecule, the unity of the animal association is to be compared with that of a village to which individuals may come, or whole families may be replaced,

or move away without replacement, and still the village retains its identity, not only in name, but by the retention of certain distinctive and more or less elusive attributes. Within this general organization of the village or of the animal community there may be all gradations from solitary to highly social individuals.

From the point of view that even so heterogenous a group as an ecological association may still be more or less closely integrated one is in much better position to study the different degrees of integration represented by the types of animal aggregations we are considering.

The first step toward social life in lower animals is the appearance of tolerance for other animals in a limited space (7) where they have collected as a result of random movements or of tropistic reactions to their environment. This may occur in connection with some phase of breeding activity but it may also be exhibited without sexual significance. Some of the less complex of these aggregations may exist because there is an absence of dissociating factors among a group of animals that have been hatched out in a restricted locality, or that have been brought together by any other process. Thus some of the aggregations resulting from tropistic responses may well owe whatever permanency they possess to the absence of disruptive factors rather than to any inherent gregarious tendency or possible advantage.

A first advance in social life is made when these groupings serve to promote the welfare of at least some of the individuals forming them, illustrated by the slower rate of moisture change in an aggregation of land isopods out of water equilibrium with the surroundings. Under conditions of drouth this results in a definite prolongation of life. Other examples are found in the preceding section.

The land isopods and *Ophioderma* have gone little beyond such a stage in their social development. There is some slight evidence of mutual attraction, but the experiments to date do not indicate how much of this would also be exhibited toward similar inanimate objects. There is also slight evidence of integrated group behavior in that the bunch shows occasional periods of activity apparently originating in one individual and passed mechanically through the group. Such activity may be the beginning of disintegration of the group, but it frequently results in a closer aggregation because the animals may move closer together during their brief period of activity.

The state of development of integration by means of which the group acts as a unit, once it appears, is obviously a very important criterion of the degree of social development that has been attained. When there is no integrative action one is dealing with a crowd, a mere collection of individuals within a limited area. Apparently it was this aspect that Szymanski (197) had in mind in distinguishing between primary reactions, the reactions of the individual, and secondary reactions, the reactions of the individuals as members of a group. On the whole the state of development of group integration appears a better criterion than Deegener's (45) touchstone, social benefit, for attempting to evaluate the degree of social life existing within a group.

1. Tactile integration

The simplest form of group integration is furnished by animals in physical contact when they respond by group behavior to tactile stimuli transmitted directly. Such integration may reach a sufficient degree of organization for the group to show synchronous behavior. *Liobunum*, the harvestman, has been ob-

served by Newman (141) to give such reactions. When first seen they covered an area about five feet in diameter and were perfectly motionless. When the observer came close they began a rhythmic stationary dance practically in unison. This died down shortly but could be reinduced by further stimulation.

When the colony was first seen the long legs of neighboring individuals were interlocked, which would sufficiently account for the transmission of stimuli through the group. It should be noted, since we are interested in the state of integration of the aggregation, that the rhythm was not perfectly synchronous at the beginning but became practically so after a few seconds.

Such integration due to tactile transmission is highly developed in the sleeping groups of bats (8), which may hang in compact clusters, as already mentioned. If one be touched the whole cluster may drop. Allen caught eighteen by holding an insect net under the group and touching only one of the outer bats.

2. *Contact-odor integration*

Sex recognition, which frequently causes animals to give characteristic group reactions, often with only two animals, is frequently accomplished by contact reactions alone (9, 11, 35, 139, 146). Among other methods of sex recognition, that due to chemical senses deserves prominent mention. This is well illustrated by the long distances certain male moths will fly to cluster about a female ready to copulate. Animals may aggregate at other than the breeding season due to the same sort of stimuli, and this stimulus is also frequently effective in maintaining an aggregation once formed; witness the classical case of *Paramecium*. Such reactions are apparently widespread and may be one factor in the maintenance of schools of fish, because some fishes seem to be able to sense the difference in chemical concentration between the center and periphery of the school, a difference which, in its turn, the school itself maintains. Much of the social organization of the ants is built on a combination of these two senses, since ants apparently live largely in what to them is a world of contact-odor forms (205).

3. *Visual integration*

Sight plays an important rôle in the integration of animal groups. When one vulture soaring aloft sees another swoop miles away, he moves over and also swoops; his reactions are seen by others and thus these scavenger groups congregegate rapidly, although they practically lack a sense of smell.

Aggregations of male frogs in the breeding season will follow and frequently tightly clasp any moving object—salamander, fish, other males, etc.—a reaction based at least in part on sight. Other instances might be multiplied, but one spectacular one, that of the synchronous flashing of fireflies, must suffice.

A considerable controversy has been waged over this subject but the observation-experiments of Hess seem to have established the fact of its occurrence (89). He found a valley of fireflies flashing in unison, with the flash apparently initiated on a hill at one side, from which it spread almost instantaneously over the valley. The next night in the same place the observer was able to obtain at least partial control of the flash, and to alter to some extent the intervals between flashes. With a pocket flashlight he gave the initiating signal just before it would normally have occurred, and the insects followed the artificial lead until the interval was reduced to three-quarters of its original duration, and then one-half.

At the second trial at one-half the original period fewer insects followed the flashlight, and after that the unison was broken.

It seems probable here that we are dealing with a phenomenon of two distinct aspects (17). One is a recovery response similar to recovery from fatigue. Such flashing would rarely be synchronous or near-synchronous. On the other hand there appears to be a releasing stimulus which, in the cases observed by Hess, might come either from the pace-setting flash of a firefly or of an electric torch. This brings up the problem of the leader in group integrations, for which we have not space here. It is discussed at some length by Child (34).

4. Integration by sounds

Among many animals group integrations occur as the result of sound production. To be sure of this one must have evidence that behavior is altered as a result of sounds. The fact that collections of animals, such as frogs or insects, are producing sounds which are loud to the human ear is not good evidence that they have group significance (124). As reported earlier, there is evidence that among some animals sounds may be used in sex recognition. Perhaps they are more often of sexual significance in general sex stimulation, which, while of advantage to the group, may yield no advantage to the sound producer and may even result disastrously in the case of young deserted by a nesting bird who has been stimulated to renewed sexual activity by the outburst of song. Such cases have been observed by creditable ornithologists (186).

Ohaus (142) and Wheeler (207) report that the *Passalus* beetles, which have the habit of boring in logs, are kept together by stridulatory signals. Wheeler has more than once spoken of his observations indicating that aerial sounds may play a part in the integration of ant colonies, but on this point there are other observations to the contrary (70).

Beebe (15) thinks that there is a close correlation between habitat and habits of tropical birds and the development of their voice, which is popularly supposed to be one of the principal attributes of tropical birds. Solitary birds, living in the open country where sight is more or less uninterrupted, he reports to have a tendency to negligible voices. Inhabitants of dense jungle, if solitary, have remarkable vocal powers, with loud staccato calls or with insistent rhythm. Such birds may be nocturnal in habit. Birds living in pairs or in families have, for the most part, vocal organs which they use to good effect, but they lack the superlative voice development of solitary birds. Birds living in flocks have voices that are still less in evidence, though there are notable exceptions to this rule, as, for example, the parrakeets.

In the matter of vocal performance, as with tactile and visual integrations, group synchronisms have been reported. The group singing of the western meadowlark is an example among birds. One of the most interesting cases is that of the snowy tree cricket, which has been much studied, and which Fulton (78) reported to effect changes in chirping rate in order to chirp in unison.

Shull (188), a careful and critical observer, concluded earlier that real synchrony does exist in the chirping of this tree cricket. Later he concluded that cases of synchronism were usually accidental but he still believed that the singing insects do influence one another. Lutz (124) is skeptical both concerning the fact of synchronism and of its importance, at least in this case.

Synchronic behavior may of course merely mean that the group, while reacting as individuals, receive the stimulus at the same time and so react simultaneously. This is illustrated by the responses Minnich (138) obtained when he exposed aggregations of caterpillars to various sounds. Such synchronism has no bearing upon the problem of group integration.

Much emphasis has been placed on the rôle played by the human voice in the integration of human society; some social psychologists prefer to define man as a language animal. In this he does not appear to be unique except in the degree to which language has been developed in his species. Craig (39), in discussing voices of pigeons as a means of social control, finds that in animals with so highly developed instincts as birds, there is still much of the social life that cannot be explained on an instinctive basis. The reaction of the individual pigeon must be adjusted to meet the activities of other birds, its parents, its mate, its young, its neighbors and chance strangers. The adjustment is very delicate and requires that each individual must be susceptible to the influence of others, an adjustment which is largely accomplished by vocal means.

Lutz recently examined the importance of insect sounds and is inclined to question strongly their having any group value among these animals. Perhaps more time has been spent on the vocal-auditory method of group integration than is justified by the conditions obtaining at the aggregation level with which this report is immediately concerned. Its interest by reason of its importance with the higher animals must be the excuse.

It is profitless to speculate at present concerning the possibility of other, more subtle methods of group integration such as the observations of Gurwitsch suggest may result from exploration in the field of biophysics.

VII. SOCIAL SIGNIFICANCE OF AGGREGATIONS

So far we have seen something of the kinds and the extent of the aggregation phenomena in the animal kingdom and of the direct and indirect forces acting to control the formation of aggregations. We have outlined the present status of our knowledge concerning the physiological effect of aggregations and have found good evidence that some such groupings may have survival value. We have just seen that there exist methods of integration, not necessarily volitional, which may serve to organize a group closely; and that different degrees of integration exist in aggregations.

It has perhaps been implied without discussion that these aggregations have social significance. The question remains to be faced directly. This should lead to an extensive review of the evidence concerning the origin of the social habit, but instead we must limit the discussion by citing summaries of generally accepted points of view and testing these against a few of the known facts.

It is generally assumed at the present time that the gregarious or social habit in animals is at bottom an outgrowth of aggregations resulting from the association of young individuals with one or both parents. In special cases or at critical periods in social evolution, it is assumed that the period of the association becomes lengthened and the family comes to react as a unit under many conditions. Some such explanation for the origin of human society is current among sociologists, who derive organized society from the family by way of the clan (97, 117).

Students of social life in insects, especially as it exists among wasps, bees

and ants, usually adopt a similar explanation for the origin of the social habit (116, 128). Thus Wheeler in his studies on ants (205, 206) and more recently in his review of social life among insects (207) regards the insect colony as a result of the extension of the natural affiliation of mother and offspring. Wheeler's particular contribution is his theory that mutual feeding (trophallaxis) is the bond that unites parents and offspring in the social insects; the mother takes larval secretions in return for supplying food to the larvae. Wheeler also shows that the social habit has arisen *de novo* at least twenty-four different times among the insects alone, in nearly that number of natural taxonomic families or sub-families belonging to five different orders.

Opposed to this more usual view is that proposed by Herbert Spencer (192–195), which is that colony life arose from the consociation of adult individuals for cooperative purposes, as among wolves and various insects, which as we have seen, may collect under certain circumstances. From these instances Spencer suggests that in some cases permanent swarms arise and that natural selection will establish such of these groupings as are advantageous. In terms of human society, this view would stress the importance of the gang, rather than the family, as a preliminary step in the evolution of the social habit. It is important to note that the gang cuts across family lines in its formation. Unfortunately for Spencer's point, which may well be correct in some instances, he illustrated his theory by a concrete example among ants that probably owe their social development to an extension of the family.

Wheeler expresses the usual attitude toward these consociations when, after describing some instances of aggregation in ants, he dismisses them as either entirely fortuitous instances, which would occur wherever ants might be abundant and places of refuge scanty, or as the manifestation of highly developed social proclivities, and not of such proclivities in process of development.

It is worth emphasizing, as Child (34) recognized, that both the congregation and the family basis of societies are in fact but two different kinds of aggregations, so that, at all events, aggregations of some sort are essential for the development of the social habit. In other words, this phase of the problem of social origins is not whether the social habit as seen among insects, birds, man, etc., arose from such aggregations as we have been discussing in earlier sections, but whether they arose from a family aggregation or from one of another type. Deegener (45) recognized this division of aggregations, which does not seem to have been understood by many writers on the subject.

Discussion of the problems of the origin of the family must be reserved, but it is at least thinkable, and there is enough evidence to warrant further inquiry, that the human family (76, 103), and perhaps all sexual phenomena among animals as well, were conditioned in their development by the previous formation of aggregations, which primarily had no sexual significance, but possessed other survival value.

The other aspect of the problem is concerned with whether or not larger social organizations always rest on family units. Observations on bird behavior furnish interesting information on this point. Spencer's theory would require that the flock be formed by the coming together of individuals; the more accepted theory would emphasize the importance of the family. The question at hand is, which of these theories actually holds true in the seasonally recurring development of bird societies?

There is evidence that birds do migrate as families (125, 135), and in the tropical rain-forests parrakeet flocks are made up of pairs rather than of individuals. With the whistling swan and Canada goose the family groups can supposedly be recognized up until mid-winter.

On the other hand Beebe (15) records the common occurrence of heterotypic flocks in British Guiana, one of which has already been cited. Similarly heterotypic flocks of migrating birds which contain only one representative of a given species are not formed from the junction of family groups. Sherman (186), a careful observer of bird habits, gives much detailed data to show that not all flocking is on the family basis. One who knows the egg-laying habits of cowbirds would expect their flocking to be by individuals. Bobolinks and goldfinches begin the formation of their autumn flocks by the congregating of old males. Chimney swifts, a pre-eminently flocking species, leave their nests by ones and twos to join the immense post-breeding flock.

Here then we have evidence that bird flocks are not always based on the family as a unit. Thus in these more highly organized groups, the individual may be the unit, just as in the aggregations of isopods and brittle starfish. It may be that the highest types of social organization, such as occur in ants and termites, with their development of different types of neuters, come about only through a persistence of family relations, but it is also true that well integrated social groupings arise merely from the aggregation of individuals.

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POLYEMBRYONY IN ANIMALS

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I. INTRODUCTION

THE fact that an egg may, under certain conditions produce two or more embryos is perhaps no more remarkable than that an egg will form a single individual. The developmental factors involved in the production of the individual embryo must be the same in both cases. Nevertheless, the discovery that multiple embryos develop from the egg of a given species has served to arouse the interest of biologists.

In the zoological literature the term polyembryony has been applied to cases in which two or more individuals develop from a single egg during the course of its early development. The term was first used by botanists, and among plant embryologists is applied to all cases in which multiple embryos are formed in the embryo sac, irrespective of the origin of the embryos. Thus in plants multiple embryos (polyembryony) may arise from two eggs, or from the splitting of one egg, or from any one of the following sources: nucellus integument, synergids, antipodal cells, endosperm cells, suspensor. Animal embryologists use the term in the restricted sense only, that is, it is applied by them to cases in which the several embryos develop from one egg.

Some objections have been offered to the term polyembryony, especially in applying it to cases of twinning in animals. But so long as the term is used in a purely descriptive sense, and without implying any particular mode of development, there can be no serious objections to its universal application. Twinning itself must be regarded as the simplest type of polyembryony. That this is true, has been demonstrated in one of the parasitic hymenoptera, to which reference is made below.

Three types of polyembryony may be recognized. These are: (1) Experimental polyembryony, or the production of multiple embryos by artificial means; (2) accidental or sporadic polyembryony, or the occasional production of multiple embryos in a species in which development is typically monembryonic; (3) specific polyembryony, or the habitual production of multiple embryos in a given species.

Among the first to produce experimentally two or more embryos from the egg was Haeckel ('69). He cut into pieces the blastulae of *Crystallodes* and obtained from the larger pieces normal larvae. Since then there have been many successful experiments of a similar nature. Among these may be mentioned the work of Wilson ('93), who isolated the blastomeres of the eggs of *Amphioxus* by shaking, and found that such separated cells were capable of forming complete embryos; the classical experiments of Driesch, and of others, on the eggs of Echinoderms; the studies of Schultze ('95), Herlitzka ('97), and Spemann ('01, '03) on Amphibian eggs; and more recently, the interesting work of Stockard ('21) in producing twins and double monsters in the fish egg by lowering the developmental rate.

The results of these, and many similar

experiments, have brought out some very significant facts with reference to the behavior of isolated blastomeres. The behavior of separated blastomeres of the eggs of different species is strikingly different. Furthermore, the blastomeres of the same species behave differently at different stages of development. Thus, isolated blastomeres of the 2- or 4-celled stage of *Amphioxus* develop into whole embryos, while a blastomere of the 8-celled stage is incapable of forming a complete embryo. The same is true of the blastomeres of the Nemertine egg. On the other hand, the isolated blastomeres of the Ascidian egg never produce a complete larva, but only partial larvae. The blastomeres of such forms are therefore not totipotent.

Apparently, these differences are dependent upon the degree of organization of the egg, or of the blastomeres at the time of their separation. For example, the undivided Ascidian egg is highly organized, and hence if the blastomeres are isolated, even at a very early stage, they are incapable of producing complete individuals, but only parts of individuals. On the other hand, in forms like *Amphioxus* the uncleaved egg is not so highly organized, and consequently the isolated blastomeres of the 2- and 4-celled stages are able to produce whole embryos. By the time the 8-celled stage is reached, the organization becomes more or less established, and each of the several blastomeres has attained a definite value as an organ-forming region, and is no longer totipotent. The results of such experiments have been used by various writers to explain polyembryony. It is probable that certain cases, especially sporadic polyembryony, may arise in nature by the accidental separation of the early cleavage cells, but specific polyembryony can not be explained in such a simple way.

Sporadic polyembryony occurs among both the invertebrates and the vertebrates. It usually appears in the form of twins, or in the closely related form of double monsters. Cases have been reported among cestodes, coelenterates, echinoderms, annelids, and arthropods, but most of the cases cited in the literature are found among the vertebrates. Twins or double monsters have been reported in every class of the vertebrates, from the lowest to the highest. Even in man it is found in the familiar cases of "identical twins."

Specific polyembryony also occurs among invertebrates and vertebrates. It has arisen independently in several distinct groups of organisms. The four outstanding cases are the following: (1) Embryonic fission in the Cyclostomatous Bryozoa; (2) Twinning in the Earthworm; (3) Polyembryony in the Parasitic Hymenoptera; (4) Polyembryony in the Armadillos.

2. EMBRYONIC FISSION IN CYCLOSTOMATOUS BRYOZOA

Among the Cyclostomatous Bryozoa there has been described a process termed "embryonic fission" which clearly belongs to the category of polyembryonic development. This process was discovered by Harmer, who first announced his discovery in 1890 in a preliminary communication to the Cambridge Philosophical Society. In 1893, after having studied the development of several species belonging to the genus *Crisia*, he published his final results. A few years later ('96, '99), Harmer extended his studies to two other genera, *Lichenopora* and *Tubulipora*. In 1903 Dr. Alice Robertson published an interesting paper entitled "Embryology and Embryonic Fission in the Genus *Crisia*." She confirmed the chief results of Harmer concerning the budding of the embryo, the separation of these buds

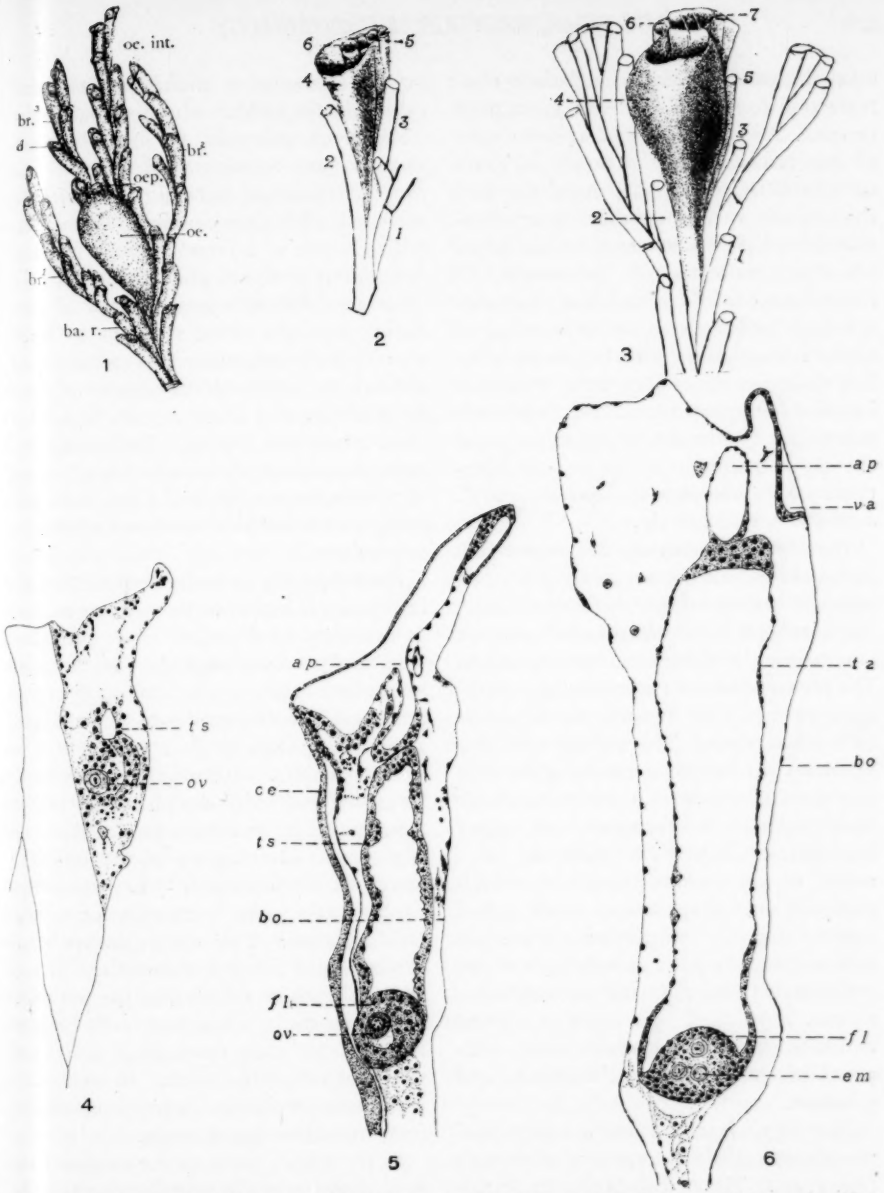


FIG. 1. A portion of a colony of *Crisia occidentalis*, showing the branching of the ooecial internode. The ooecium is the fifth member of the internode. (Robertson).

FIGS. 2 AND 3. Two stages showing the development of the ovicell in *C. remosa*. The ovicell is numbered 4 in each figure. (Harmer).

FIG. 4. A median longitudinal section of a young ovicell of *C. eburnea*. The ovum is partially surrounded by a polypide-bud. (Harmer).

FIG. 5. A similar section of *C. remosa*, showing the ovum surrounded by the follicle formed from the polypide-bud. *ap.*, aperture; *c.e.*, calcified ectocyst; *b.o.*, back of ovicell; *t.s.*, tentacle-sheath; *fl.*, follicle; *ov.*, ovum. (Harmer).

FIG. 6. *C. remosa* showing the 3-celled stage of the embryo. (Harmer).

from the mother embryo, and their ultimate transformation into free swimming larvae. She also added several new points of interest, such as the origin of germ cells, and the establishment of the fact that certain species are dioecious. Robertson worked on four species of the genus *Crisia: C. geniculata, C. occidentalis, C. edwardsiana, and C. franciscana.* Unfortunately, in her paper on the embryology of *Crisia,* Robertson incorrectly identifies the last three species. This error was corrected several years later in her systematic paper (1910). In the embryology paper the three species in question were identified as *C. eburnea, C. cornuta, and C. occidentalis,* respectively.

The Bryozoa, which are sometimes called moss-animals, are mostly marine, and are usually colonial. Superficially, they resemble hydroids, but in structure are strikingly different from hydroids. The phenomenon of polyembryony occurs quite generally throughout the sub-order of Cyclostomata. The colonies of this sub-order are characterized by great simplicity of structure. In the genus *Crisia* each colony is composed of many branches. A branch is made up of a series of internodes, each of which possesses several calcareous tubes, called zooecia (fig. 1). Within each zooecium is found the polypide, or soft parts of the individual. The polypide consists of a mouth, surrounded by a circle of ciliated tentacles, and an alimentary canal, composed of the oesophagus, stomach, and intestine.

The egg develops in a specialized zooecium, called an ooecium or ovicell (fig. 1, *oe*). The ovicell begins its formation at a very early stage of the zooecium. It is the result of a successful union between an ovum and the young polypide-bud. The ovum becomes united to the base of the stomach of the polypide-bud by the means of a strand of mesoderm called the funiculus. If the union is successful, the polypide, as such, becomes aborted, later forming a "follicle" about the developing embryo. The fertile zooecium then develops into an ovicell, which serves as a brood chamber for the developing embryos and larvae. Under these conditions the egg, instead of producing a single larva, proceeds to fragment or bud; each bud, either secondary or tertiary, or embryo develops into a larva. In this manner a single egg may produce more than 150 larvae. The secondary embryos remain within the ovicell until they have become ciliated larvae, and upon being set free each is capable of forming a new colony.

The following account of polyembryony in Bryozoa is based chiefly on *Crisia remosa,* as described by Harmer. It is probably true, as Robertson suggests, that some of his earliest stages do not necessarily represent eggs which would have produced embryos (*e.g.*, figs. 4, 5).

The germ cells. According to Robertson ('03), the germ cells in *Crisia* arise in the mesodermal layer and are produced at the edge of the growing tip of the terminal internode of the colony. They are differentiated at a point lying anterior to the budding zone. This occurs earlier than the origin of the polypide-buds. In the male colonies of a dioecious species, such as *C. occidentalis,* a few germ cells become attached to each developing bud, and thus give rise to the testis. In most cases the testis probably degenerates before forming mature spermatozoa.

In the female colonies the ovaries likewise develop at the anterior edge of the young tips, and, as in the male colonies, the germ cells must unite with a polypide-bud in order to mature. Many ova never form this union, and consequently soon degenerate. In some cases the polypide-

bud develops, while the attached ovum degenerates, either before or after having passed through the first cleavage stages. In other cases the attached ovum gains the ascendency, while the polypide-bud becomes aborted, and forms a follicle about the growing embryo.

The ovicell. As already stated, the ovicell is a specialized zooecium in which the development of the embryo takes place. Smitt ('65) was the first to show that the ovicell forms in a manner similar to that of the zooecia, but to Harmer ('93) belongs the credit of having pointed out that it is the morphological equivalent of a zooecium. In *C. remosa* the growing ovicell occupies the fourth unit of the young internode, the rest of the units being ordinary zooecia. In *C. eburnea* ovicell-bearing internodes have six zooecia and the ovicell. The latter takes the place of the second or third zooecium in an internode having no ovicell. Figures 2 and 3 show two stages in the development of the ovicell in *C. remosa*. The positions of the ovicell and the ordinary zooecia are indicated by the numbers. The ovicell is number 4 in each figure.

Fertilization and cleavage. The processes of maturation and fertilization have never been observed, but it is assumed by Harmer that inasmuch as mature spermatozoa are formed, fertilization must occur normally. Robertson believes that if fertilization does occur, it must take place near the time at which the ovum and the polypide-bud unite. In view of the probable degeneration of the testis, she suggests the possibility of parthenogenetic development.

The cleavage divisions occur while the ovicell is still undergoing development. At the time the ovum becomes surrounded by the polypide-bud the tentacle-sheath is scarcely developed (fig. 4, *ts*). In figure 5 is shown a stage in which this sheath has increased considerably in size, while the ovum is still undivided. The polypide-bud has been transformed into a "follicle," in which the cells are arranged about the ovum in concentric layers. Soon after this stage the ovum begins to divide, apparently irregularly, to form blastomeres. A three-celled stage is shown in figure 6. The three blastomeres are separated from one another and an ingrowth of follicular cells has migrated in between them. It is characteristic of all of the early cleavage stages of *Crisia* for the blastomeres to become completely separated.

The interpolation of follicular elements between the cleavage cells is a characteristic feature of the early development of *Crisia*, and as a result, the blastomeres undergo division independently of one another, that is, there is no regularity in the succession of cleavage cells. The process of segmentation continues in this manner until about twenty to twenty-four cells are formed, after which the blastomeres become collected into a compact mass. In the meantime, important changes have taken place in the growth of the ovicell. The tentacle-sheath has grown to such a size that it now practically fills up the entire cavity of the ovicell, and the follicle likewise has greatly increased, producing knob-like projections that extend into the cavity of the tentacle-sheath.

The nutriment for the rapid growth of these parts is obtained very largely at the expense of the neighboring zooecia. These have a series of intercommunicating channels which are formed by means of strands of funicular tissue that pass through pores perforating the calcareous ectocyst. The ovicell and its contiguous zooecia likewise communicate by the organic connections and through these channels the nutriment for the rapidly

growing embryo and follicle is drawn from the zooecia, which sometimes atrophy as a result. It is only in this manner that one can give a rational account of the rate of development of the ovicell, and can further explain the formation of a massive primary embryo from the minute egg of *Crisia*.

The primary embryo. The separation of the blastomeres during the earliest stages of development is undoubtedly associated with the nutrition of the embryo, and the collecting together of the cells at a later period to form the ball-stage is due to the dissociation of the interpolated follicular elements to form nutritive material which is consumed by the embryo. During this period, the embryo gives no evidence of differentiating into germ layers, but consists of a mass of protoplasm containing scattered cells and nuclei.

The ball-stage is constant for all Cyclostomata. For some time the embryo remains practically unaltered, but the surrounding follicle is transformed from a solid structure to a protoplasmic retic-

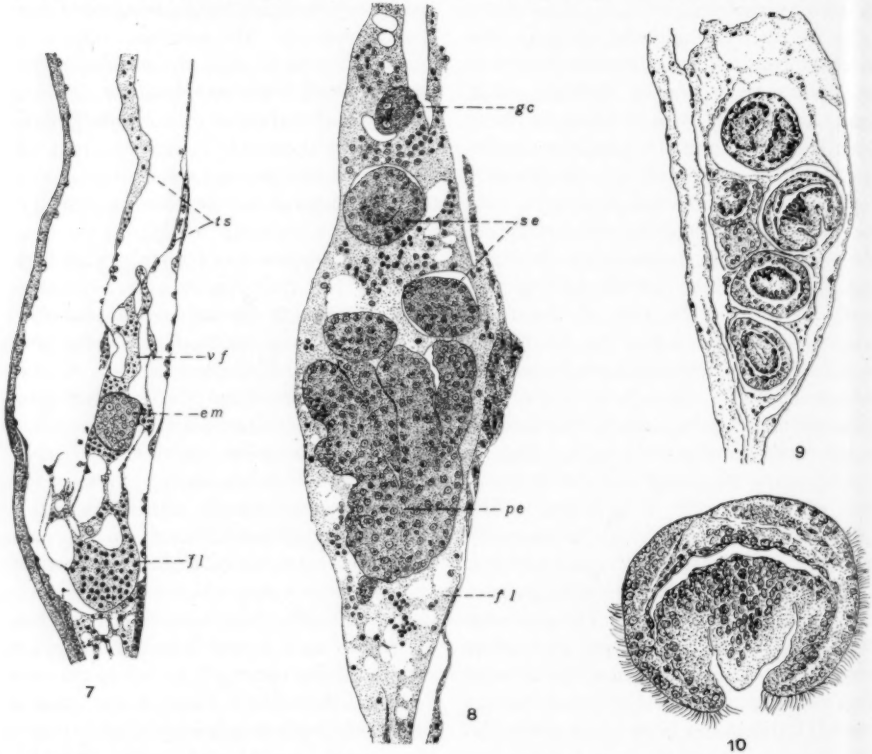


FIG. 7. *C. remosa* showing the embryo (*em*) lying in the vacuolated follicle. (Harmer).
FIG. 8. *C. remosa*. Median section showing the follicle, which has become a dense protoplasmic reticulum. The primary embryo (*p.e.*) has become a budding organ, giving rise to numerous secondary embryos (*s.e.*) (Harmer).
FIG. 9. *C. eburnea*. Median section, showing late embryos and young larvae. Original.
FIG. 10. One of the larvae from fig. 9 greatly enlarged. Original.

ulum (fig. 7, *fl*), which eventually fills up a large part of the cavity of the ovicell. The formation of the reticulum is first seen in the development of vacuoles in the solid follicle. In the organization of the protoplasmic reticulum from the follicle is to be seen the formation of a nutritive mechanism for the numerous larvae which will later arise from the primary embryo. The primary embryo itself is formed from the ball-stage by an increase in size of the latter. In some species this increase in size may enlarge the ball from 40 to as much as 200 microns.

The secondary embryos. The secondary embryos arise by a process of budding from the primary embryo, which becomes a distinctly budding organ. The simplest type of budding occurs in *C. remosa* and in *C. denticulata*. In *C. remosa* the distal end of the primary embryo sends upward several finger-like processes, which by a series of constrictions bud off secondary embryos into the reticulum (fig. 8, *s.e.*).

A variation of this simple method of budding is found in *C. occidentalis*. In this species buds may arise at any point on the surface of the primary embryo. In *C. franciscana* still another method of budding is found. The primary embryo first breaks up into relatively large masses of cells, or secondary embryos, and these in turn give rise to budding centers from which tertiary embryos are formed.

In all of these species the budding organ continues active during the entire functional period of the ovicell, even until some of the older secondary embryos have matured into free-swimming, ciliated larvae. Ultimately, the primary embryo itself forms a larva.

The larvae. Soon after the secondary (or tertiary) embryos are cut off from the primary embryo or budding organ, they differentiate into a two-layered condition, and undergo further development within vacuoles of the protoplasmic reticulum. There are also found in some of the vacuoles the "giant-cells," which are multinucleated elements formed from the thickened distal end of the tentacle sheath. Apparently, they perform the function of excavating spaces in the follicular tissue in which the larvae can undergo development.

Of the two layers of which the young larva is composed, the inner one, according to Harmer, is probably mesoderm. The free-swimming larva is completely developed within the ovicell, and at maturity has a cylindrical-shaped body with an aperture on one side that leads to the sucker (figs. 9, 10). It is composed of the two layers, and has the greater portion of the outer surface covered with long cilia. Upon reaching maturity, the larvae puncture the membrane covering the tubular aperture of the ovicell and thus escape into the surrounding medium. Here each larva is capable of attaching itself to some object by means of the sucker, and of producing a colony characteristic of the species to which it belongs.

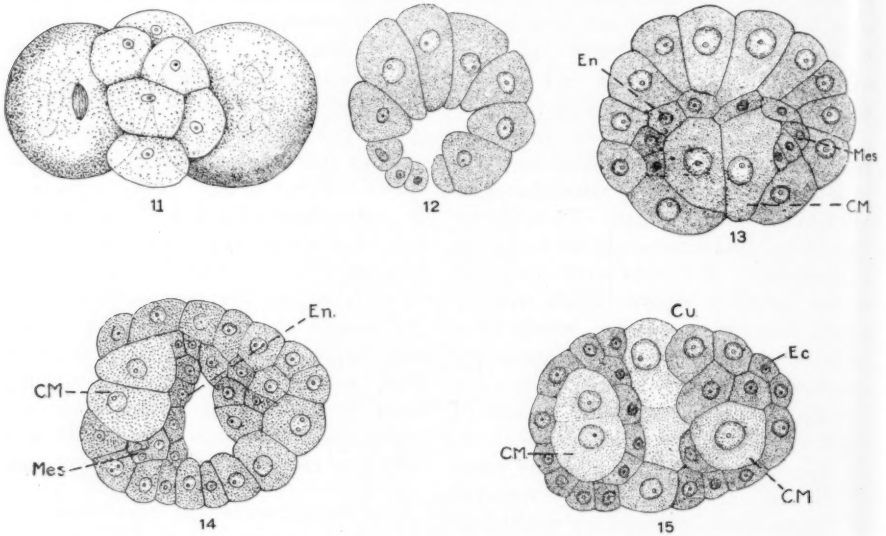
3. TWINNING IN THE EARTHWORM

The formation of twins in the earthworm deserves consideration in any general review of polyembryonic development, even though it has not been demonstrated that all of the eggs of the species concerned show this method of development. Several different investigators have reported the discovery of embryonic bifurcation in the Oligochaeta, since Dugès first observed and described a double monster of *Lumbricus trapezoides* in 1828. All of the cases so far reported, with the exception of two, fall within the highest family of the Oligochaeta, namely, the Lumbricidae. In 1921 Welch reported the occurrence of bifurcation in the embryos of one of the common tubi-

ficids, *Tubifex tubifex*, belonging to the family Tubificidae. Penners ('24) has recently described the development of double embryos in *Tubifex rivulorum*. Hague ('23) reports the discovery of bifid embryos in *Sparganophilus eiseni*, thus adding a third family (Glossocolecidae) in which this type of development is found.

first changing into flattened plates and finally disintegrating completely.

The cleavage of this egg, like that of many other earthworm eggs, is variable, and consequently it was not possible for Kleinenberg to follow accurately the early history of development. The first division produces two large blastomeres and while there sometimes follows a three-



FIGS. 11–15. EARLY STAGES OF *Lumbricus trapezoides* (AFTER KLEINENBERG)

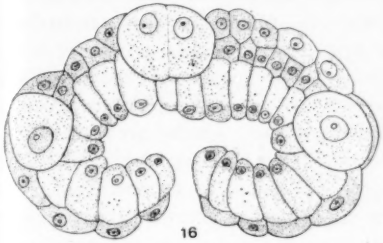
Fig. 11. Early cleavage stage seen from above, showing two large and six smaller cells. Fig. 12. Section of the blastula stage, or "germinal bladder." Fig. 13. Section of solid germinal sphere, showing the rudiments of the layers of the first embryo. Fig. 14. Late stage in which the formation of the second embryo has begun. Fig. 15. Section of young twin embryos. The one on the right is farther developed than its co-twin on the left.

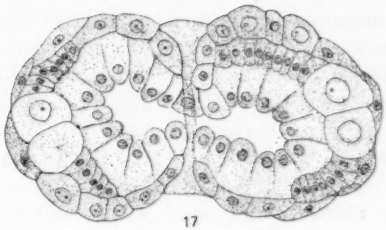
For our knowledge of the early development of twins in earthworms we are dependent almost wholly upon the account of Kleinenberg ('78, '79) on the embryology of *Lumbricus trapezoides* (*Helodrilus caliginosus trapezoides*). He found that while the number of eggs deposited in the cocoon, or egg capsule of this species varies from three to eight, yet a single egg usually developed. The rest of the eggs apparently are not fertilized, and soon undergo degeneration,

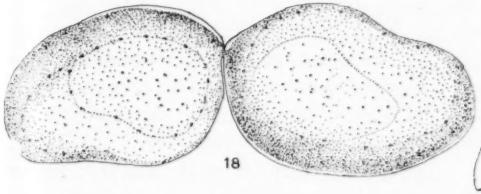
celled stage, the general rule is for each of the two blastomeres to give off in succession three small cells. The six small cells thus formed come to lie above and between the two larger blastomeres (fig. 11). By a series of somewhat irregular divisions, affecting the large as well as the smaller blastomeres, the egg develops into a blastula, or "germinal bladder." This blastula is remarkable for having its cavity, the blastocoel, frequently open to the outside by a cleavage-pore, situated

at the lower pole (fig. 12). The blastula is soon transformed into a solid sphere (fig. 13). This is brought about through the differentiation of two large cells (primary mesoblasts) which push into the cavity and become covered over by small blastomeres. From these cells the first rudiments of the entoderm and mesoderm are derived. The cell mass then elongates in the direction of the two poles. While mesoblasts (fig. 14, *c.m.*) develops somewhat in advance of the opposite end, but eventually both ends become equally well differentiated (fig. 15).

Gastrulation takes place by an invagination of the entoderm. This process begins at the lateral margins of the furrow or groove in both hemispheres, and results in producing two gastrulae, which are held together by the median cord of large







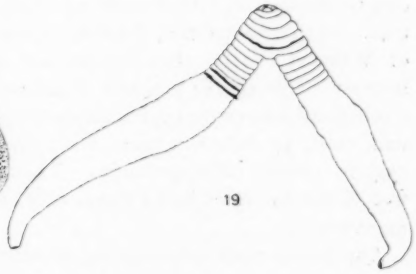


FIG. 16. Longitudinal section of a double embryo, in profile (After Kleinenberg).
FIG. 17. Longitudinal horizontal section of a double embryo (After Kleinenberg).
FIG. 18. Two embryos about to break apart. Original.
FIG. 19. Double monster, produced as a result of the failure of the embryos to separate from each other. Original.

the elongation of the egg is in progress, a transverse furrow appears, mid-way between the two poles. This furrow does not extend around the entire circumference, but cuts in from one side only. The furrow continues to deepen until finally the two hemispheres of the egg are held together only by a few enlarged ectodermal cells (fig. 15, *cu*). In the meantime, the cell mass undergoes further differentiation. The end containing the large primary ectodermal cells (fig. 16, 17). While thus connected, the two embryos complete their internal organization and development. They usually succeed in freeing themselves from each other by a series of rotations (fig. 18), which result in breaking the attenuated, connecting cord. If for any reason the cord should fail to break, double monsters, showing various degrees of union, are produced (fig. 19).

A second type of abnormality is some-

times found during the gastrula stage. It consists in the formation of a small bud on the margin of the mouth of the gastrula. It is probably the result of a very unequal development of the two halves of such stages as that shown in figure 14.

A survey of the literature on the occurrence of twinned embryos in earthworms indicates clearly that in most of the species studied twinning is rather rare. The species in which it has become a common phenomenon is *Lumbricus trapezoides*, now known as *Helodrilus caliginosus trapezoides*. Indeed, Kleinenberg regarded the gemelliparous development in this species as universal. On the other hand, Vejdovsky ('88–'92) maintained that the development of two embryos from one egg is abnormal; he therefore suggested the possibility that the abnormal development may be due to changes in temperature and moisture. In this connection, the observations of Weber ('17) on this species are of interest. Out of 184 cocoons examined, 1 contained four embryos, 101 two individuals each, 57 only one each, and 25 had eggs in various cleavage stages. Thirty-five of the 101 cases had various types of monsters.

Any future work on twinning in earthworms should involve a study of a much more complete series of early stages than any previous worker has been able to obtain, chiefly with the view of finding a possible relationship between the cleavage phenomenon and the twinned embryos. Furthermore, in the light of Vejdovsky's suggestion, such studies should include experiments carefully planned to determine what influence, if any, changes in temperature, moisture, and air may have on the production of double embryos.

4. POLYEMBRYONY IN THE PARASITIC HYMENOPTERA

Since the discovery of polyembryony in insects by Marchal in 1898, there have appeared a number of papers dealing with this type of development in the parasitic Hymenoptera. Marchal's main paper ('04) gave the first clear description of polyembryony. It presents an account of the development of *Encyrtus fuscicollis* and *Polygnotus minutus*, together with the suggestion that *Ageniaspis testecipes* must also develop by polyembryony.

In 1906 Silvestri published a very important paper on the development of *Litomastix truncatellus*. He demonstrated that the egg of this parasite produces on the average about 1500 sexual individuals, in addition to a number of the so-called asexual larvae which are non-viable. Following this, Silvestri issued a series of papers dealing with the embryology of various species of parasitic Hymenoptera, both monembryonic and polyembryonic.

In 1914, Martin published a paper on *Ageniaspis fuscicollis*. This paper deals with the very early stages of the egg.

In 1915 the writer published an account of the late stages of development of *Copidosoma gelechiae*, and since then a series of papers covering the development of *Paracopidosomopsis floridanus*. The latter, a common parasite of the cabbage looper *Autographa brassicae*, was described by Ashmead as a distinct species, but according to Leiby ('22, p. 198), Dr. L. O. Howard, Mr. A. B. Gahan, and others regard this species as identical with *Litomastix* or *Copidosoma truncatellum*. A short paper dealing with the biology and sex ratios of *Platygaster felti*, a species which also develops by polyembryony, was published in 1921.

In 1922 Leiby published a very complete account of the polyembryonic development of *Copidosoma gelechiae*. Leiby and Hill ('23, '24) have described the development of two species belonging to the family Platygastridae, namely, *P. hiemalis* and *P. vernalis*, both of which are parasites of the Hessian fly.

In addition to the above publications, there are many references in the literature to species some of which undoubtedly develop by the process of polyembryony. In the following table (table I) an attempt is made to include all of the undoubted polyembryonic species. The first column gives the name of the polyembryonic species, the second the name of the host insect, the third the average number of individuals in a brood, and the fourth the observer.

TABLE I

PARASITE	HOST	BROOD	OBSERVER
Platygaster hiemalis	*Phytophaga destructor*	2	Leiby and Hill, '23
Platygaster vernalis	*Phytophaga destructor*	8	Leiby and Hill, '24
Platygaster felti	*Walshomyia texana*	11	Patterson, '21
Platygaster felti	*Rhopalomyia sabinae*	18	Patterson, '21
Polygnotus minutus	*Phytophaga destructor* *Phytophaga avenae*	11	Marchal, '04
Ageniaspis fusciollis subspecies *praysincola*	*Prays oleelus*	14	Silvestri, '08
Ageniaspis testaceipes	*Lithocolletis cramerella*	13	Marchal, '04
Ageniaspis fuscicollis	*Hyponomentus malinellus*	100	Marchal, '04
Encyrtus variicornis	*Anarsia lineatella*	28	Sarra, '15
Copidosoma buyssoni	*Coleophora steffani*	58	Silvestri, '14
Copidosoma sp.	*Olethreutes variegana*	148	Sarra, '18
Copidosoma gelechiae	*Gnorimoschema gallaesolidaginis*	163	Leiby, '22
Copidosoma gelechiae	*Gnorimoschema salinaris*	191	Patterson, '15
Paracopidosomopsis floridanus	*Autographa brassicae*	1161	Patterson, '17
Litomastix truncatellus	*Plusia gamma*	1481	Silvestri, '06
Copidosoma tortricis	*Tortrix comariana*	?	Waterson, '22
Berecyntus bakeri	*Euxoa auxiliaris*	1289	Snow, '25
Aphelopus theliae	*Thelia bimaculata*	50	Kornhauser, '19

The species listed in the table belong to three families of the parasitic Hymenoptera, namely Encyrtidae, Platygastridae, and Dryinidae. Further investigations will undoubtedly bring to light many additional polyembryonic species. The reviewer has observed four or five unidentified species in which certain phases of development strongly suggest that they are polyembryonic.

There are many points of similarity in the method of development as found in the several species so far investigated, but there are also striking differences. Many of the accounts so far given for the development of polyembryonic insects are incomplete, and for this reason it is difficult to prepare a review covering such important questions as the origin and evolution of this type of development in the Hymenoptera. However, the recent observations of Leiby and Hill ('23) indicate that polyembryony in insects begins as a twinning process, in which the egg, at an early stage, divides into two parts, each of which ultimately forms a complete individual. As the number of individuals arising from the egg (of different species) increases, the process becomes more and more complicated, finally culminating in a highly specialized mode of development. It will be necessary, perhaps, to study in detail the development of several more species before a correct view of the evolution of polyembryony in insects can be reached. In

the meantime, it is possible to indicate in outline the general trend of the process in this group. This can be done best by considering first twinning in the egg of *Platygaster hiemalis*.

Twinning in Platygaster hiemalis

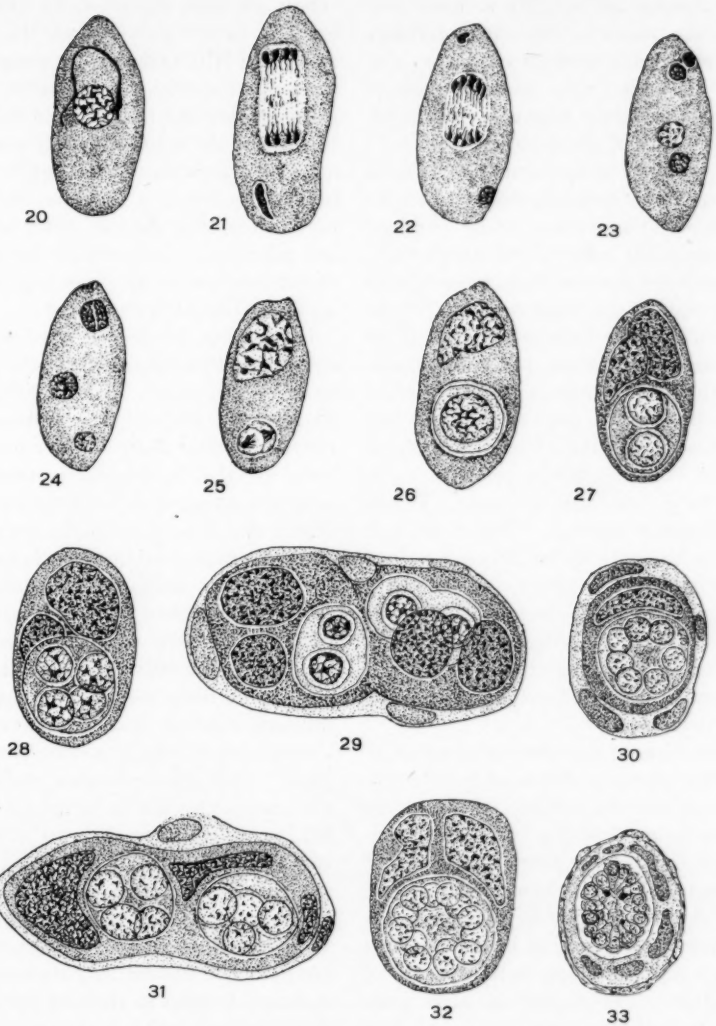
Platygaster hiemalis is a parasite of the Hessian fly, the well-known pest of wheat. Leiby and Hill ('23) have shown that its egg develops either monembryonically or polyembryonically. The parasite lays from four to eight eggs in the egg or young larva of the host. Some of these eggs give rise to single embryos, others develop into twins, while still others degenerate. Some eggs of the group of four to eight are inseminated, while others are unfertilized.

The freshly deposited egg is ovoid in shape, with a rounded posterior end and a somewhat pointed anterior end. The spherical nucleus is situated near the center of the egg. If the egg is fertilized, a single elongated sperm is present in the cytoplasm (fig. 20). But whether fertilized or not, the egg undergoes two typical maturation divisions, during which reduction in the number of chromosomes occurs (figs. 21, 22). The two polar body nuclei are not eliminated from the egg, but remain for a while as condensed masses at its anterior end (fig. 23). They soon unite to form a very large, single polar nucleus, or the paranucleus of Marchal (figs. 24, 25).

After maturation is completed, the female pronucleus moves toward the posterior end of the egg, where it unites with the sperm nucleus to form the cleavage nucleus, or in case the egg is unfertilized, the female pronucleus becomes directly the cleavage nucleus. Apparently, the presence of the sperm in the cytoplasm does not modify either maturation or the type of development which follows. Fertilization does, however, determine the sex of the resulting individuals, for in common with many other hymenoptera, the unfertilized eggs of polyembryonic species give rise to haploid males, developing by what has been called facultative parthenogenesis. The fertilized egg presumably gives rise to females. This point, however, has not been fully established.

About twenty-four hours after the beginning of development, the egg becomes differentiated into two distinct regions, the polar region and the embryonic region. The embryonic region, which eventually gives rise to the embryos, is situated in the center of the posterior half of the egg. It stains lighter than the rest of the egg and contains the cleavage nucleus (fig. 26). All of the rest of the egg comprises the polar region, in the anterior portion of which is found the large paranucleus. The polar region has been termed the trophamnion, chiefly because of its function of absorbing and elaborating the host tissues for the purpose of nourishing the parasitic embryos until they are able to feed for themselves. The absorption of food from the host tissue is facilitated by the change which takes place in the distribution of the several parasitic eggs. Sometime during the early part of the second day the group of from 4 to 8 eggs deposited in the host by the parasite becomes dispersed throughout the body cavity of the host embryo or larva, and during the process of scattering each egg comes in contact with certain host tissues which partially or wholly surround it. The eggs are now called parasitic bodies. About one-third of the eggs deposited do not develop, apparently because they fail to become surrounded by the tissues of the host.

Just prior to the division of the embryonic or cleavage nucleus the polar



FIGS. 20–33. SHOW VARIOUS STAGES OF THE DEVELOPMENT OF THE EGG OF *Platygaster hiemalis* (AFTER LEIBY AND HILL)

Fig. 20. Egg showing nucleus and sperm. Fig. 21. Egg four hours old showing sperm and first maturation spindle. Fig. 22. Egg seven hours old, showing second maturation spindle, first polar body (above), and sperm nucleus. Fig. 23. Egg shows the two polar bodies, and the male and female pronuclei. Fig. 24. Same as above except that polar-body nuclei are fusing. Fig. 25. Egg with pronuclei fusing and large polar nucleus. Fig. 26. Egg showing the embryonic region differentiated from rest of cytoplasm. Fig. 27. Parasitic body three days old, with two nuclei in embryonic area, and two paranuclear masses. Fig. 28. A parasitic body with four embryonic nuclei. Fig. 29. A longitudinal section through the twinning stage. The embryonic region has divided and each half has received two nuclei. Fig. 30. Embryo in early blastula stage. Seven of the sixteen nuclei are seen in the section. Fig. 31. A twin germ, which is surrounded by the cyst of host tissue. The trophamnion has not yet divided. Fig. 32. A 32-celled blastula of an egg developing monembryonically. Fig. 33. Late blastula stage of embryo.

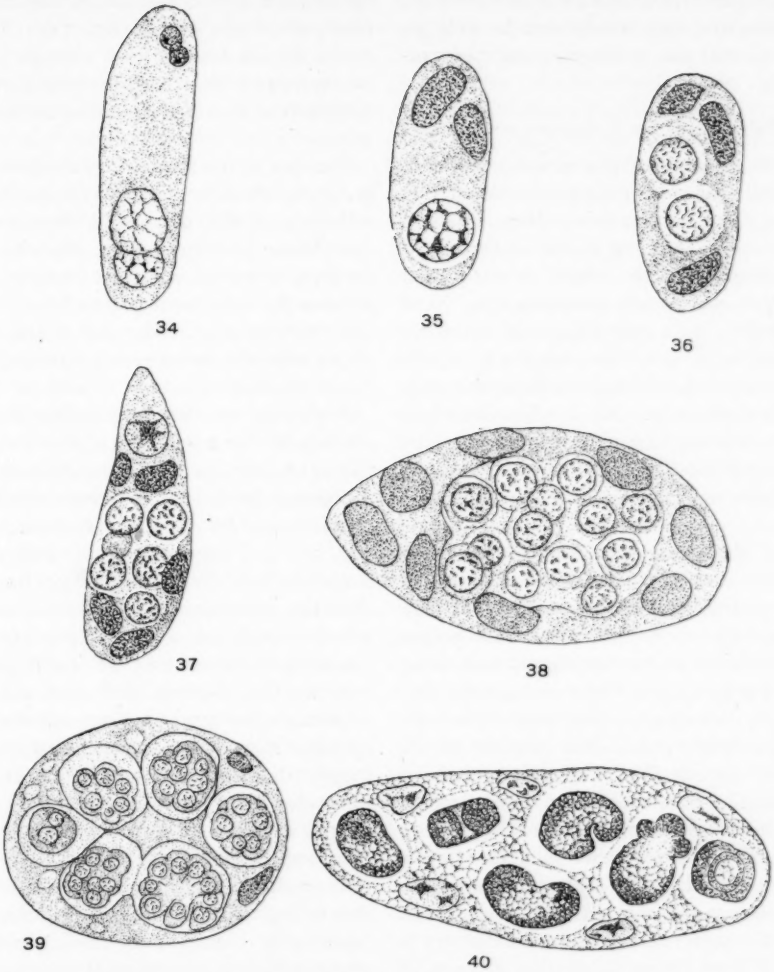
nucleus divides amitotically to form two paranuclear masses. The first division of the embryonic nucleus occurs on the second day (fig. 27), and the second divisions take place between the fourth and fifth days of development (fig. 28). At this point one of the paranuclear masses migrates to the posterior end of the parasitic body and divides, while the one remaining at the anterior end also divides. There are now four of these masses, two at each end of the trophamnion. These divisions result in changing the shape of the parasitic body from oval to elongate. Evidently, this change in shape is one of the developmental steps leading to the production of twins, for the parasitic bodies in which it occurs proceed immediately to divide into two parts, each of which forms an embryo. The embryonic region is the first to be affected by the division. It divides into two equal parts, each part receiving two of the four embryonic nuclei (fig. 29). Each half of the divided embryonic region constitutes a true germ, which will eventually develop into a parasite.

The division of the embryonic region to form two germs is followed by the appearance of a constriction about the middle of the trophamnion (fig. 29). This constriction finally completely divides the trophamnion, and although the two halves thus formed are held together for some time by the cyst of host tissue, yet the two germs develop independently of each other. The nuclei of each germ divide to produce four (fig. 31), then eight and finally sixteen nuclei. The sixteen nuclei arrange themselves in the form of a hollow sphere, thus forming a typical early blastula stage (fig. 30). In the course of further development, the embryonic nuclei continue to divide, and cell walls come in to change the early blastula into a cellular blastula (fig. 33).

Not all eggs deposited by the female parasite produce twin embryos, but as Leiby and Hill have shown, some develop monembryonically. Apparently, all of the eggs develop in a similar manner up to the point at which four embryonic nuclei are present. If the egg is to form but one embryo, a division of the embryonic region at the four-celled stage does not take place, but instead the cleavage nuclei continue to multiply (fig. 32) until a single blastula is developed.

It will not be necessary to follow in detail the development from the blastula to the adult stage. The embryos reach an advanced stage of development during the fall months, and pass the winter in the body of the host. Their development is continued again in the early spring, and during the latter part of the spring, each embryo, upon attaining the larval stage, ruptures the trophamniotic membrane. The free larvae feed upon the host tissues, finally consuming the entire contents of the host. The fully formed larvae remain within the body wall of the host during the early summer, and each embryo forms a pupal cell in which it transforms into a pupa. The adult parasites emerge from the host carcass and puparium in the early fall, at a time when they are able to find and parasitize freshly deposited eggs of the second generation of the Hessian fly.

The type of development exhibited in *Platygaster hiemalis* is of very great importance to the subject of polyembryony in insects. Interest in the case does not rest alone on the fact that it shows the simplest possible type of polyembryony, but also on the fact that some of the eggs develop monembryonically. The monembryonic development in this species is similar to that described for certain monembryonic platygastrids, and represents a very highly specialized type of development. It is probable that without the development



FIGS. 34–40. SHOW SEVEN STAGES IN THE DEVELOPMENT OF *Platygaster vernalis* (AFTER LEIBY AND HILL)

Fig. 34. A stage showing the fusion of the pronuclei. The two polar bodies are at the upper end. Fig. 35. The embryonic region is differentiated about the cleavage nuclei. The polar body nuclei have become paranuclear masses. Fig. 36. A parasitic body with three paranuclear masses, and the cleavage nucleus ha divided. Fig. 37. A parasitic body five days old, showing five of the eight embryonic nuclei. Fig. 38. A section of a parasitic body, showing thirteen of the sixteen germs. Fig. 39. A section of a thirteen day old polygerm, showing portions of six embryos. Fig. 40. Longitudinal section of a polyembryonal mass about 26 days old.

of this specialized type of monembryony, the parasitic egg would not be able to proceed to the production of polyembryony.

Polyembryony in Platygaster vernalis

A knowledge of the simplest type of polyembryony in *Platygaster hiemalis* is essential to an understanding of that process as it is found in the more highly specialized forms. All investigators familiar with insect polyembryony have recognized the desirability of working out the development in a species in which but a few individuals arise from one egg, say four or eight. No one has described a species with four embryos, but recently one in which about eight embryos develop has been reported on by Leiby and Hill ('24).

The species in question is *Platygaster vernalis*, and like *P. hiemalis* is also a platygastrid infesting the egg of the Hessian fly. While there are many points of similarity in the development of these two parasites, yet there are certain significant differences. The chief differences are as follows: (1) The female of *P. vernalis* deposits but a single egg at each oviposition instead of from four to eight; (2) the parasite egg is placed in the egg of the host in a manner such that it becomes lodged in the mid-intestine of the host larva; (3) the parasitic body of *P. vernalis* never becomes surrounded by a cyst of host tissue; (4) finally, the egg of *P. vernalis* produces on the average about eight embryos, and does not develop monembryonically or produce twins.

The early stages of *P. vernalis* are very similar to those of the preceeding species. The egg is cylindrical in shape and contains the oocyte nucleus and if it has been fertilized, there is present in the cytoplasm a single spermatozoon. The two typical maturation divisions occur, giving rise to two polar-body nuclei (fig. 34). These nuclei do not fuse to form a single polar nucleus, but instead each becomes directly transformed into a paranuclear mass (fig. 35).

The egg is transformed into a parasitic body shortly after the cleavage nucleus is fully organized (fig. 35). A clear area of cytoplasm develops about the cleavage nucleus, and this with the nucleus constitutes the embryonic region from which the embryos arise. The rest of the cytoplasm with the two paranuclear masses is the trophamnion.

Beginning on the second day and extending to the seventh day after oviposition, the cleavage nucleus undergoes four divisions, producing a series of stages characterized by two (fig. 36), four, eight (fig. 37) and sixteen (fig. 38) embryonic nuclei respectively. It sometimes happens that the embryonic nuclei do not divide synchronously at a given division, and consequently there may be less than sixteen nuclei. During this time the trophamnion increases in size and the paranuclear masses also multiply and become evenly distributed throughout the trophamnion (fig. 38). At the end of the fourth division of the embryonic nuclei the parasitic body develops into a typical polygerm. Each embryonic nucleus, after separating from the other, becomes surrounded by a small amount of cytoplasm, about which a cell membrane is formed. A cell thus organized is a germ that will eventually give rise to one or two embryos.

The nucleus of the single-cell germ multiplies by division until eight nuclei are formed when a division of the germ to produce two daughter germs may occur. Not all germs, however, divide. If a daughter germ divides the result is the

formation of a pseudogerm, or small germ which is not capable of further development.

During an early stage of the polygerm strands from the peripheral trophamnion pass toward the center of the polygerm and surround the developing germs or early blastulas (fig. 39). The subsequent stages of development are similar to those of *P. hiemalis*. However, not all of the embryos reach full development, so that the polyembryonic brood averages only about eight individuals. After the primary larval stage is reached, the trophamniotic membrane ruptures, and the free larvae feed upon the chyle or contents of the mid-intestine of the host. The mid-intestine finally ruptures and the so-called secondary or mature larvae feed upon the tissues of the host.

Polyembryony in other species

A knowledge of the primitive types of polyembryony as just outlined for *P. hiemalis* and *P. vernalis* is necessary for an understanding of the more complex types of polyembryony as found in other Hymenoptera, in which from 150 to more than 2000 individuals arise from one egg. The development of three of these complex forms has been worked out in more or less detail. These are *Copidosoma gelechiae* (Patterson, '15; Leiby, '22), *Litomastix truncatellus* (Silvestri, '06), and *Paracopidosomopsis floridanus* (Patterson, '21b). The average numbers of embryos produced per egg in the three forms are 163, 1481, and 1161, respectively (see table I).

The detailed accounts of the development of the complex forms antedate those given for the simpler species. It is now evident that it will be necessary to reinvestigate or reinterpret some of the late stages of development of such forms as *P. floridanus* and *L. truncatellus*. However, sufficient evidence is available to show that as the number of embryos per egg increases the polyembryonic process becomes more and more complicated. A comparison of the development of *P. vernalis* with that of *C. gelechiae* shows that each true germ of the former develops directly into an embryo, usually without division, while in the latter each multinucleated morula of the late polygerm stage always divides to give rise to two morulas, and hence to two embryos (Leiby, '22). Moreover, during the formation of the polygerm of *C. gelechiae*, there is an extensive multiplication of the embryonic nuclei before the primary germs are organized, and when they are formed, by groupings of these nuclei, their number is comparatively large. This, together with the fact that each morula divides to produce two embryos, accounts for the greater number of embryos arising from the egg of *C. gelechiae*.

In *Paracopidosomopsis* the polyembryonic process is even more complicated than in *C. gelechiae*, but Leiby and Hill ('23) who have also examined this species, believe that the secondary morulas divide to form tertiary morulas which then differentiate into larvae.

In this brief review of the development of the complex types many of the details have necessarily been omitted, but it is hoped that sufficient have been given to indicate to the reader the course of polyembryony in the Hymenoptera.

5. QUADRUPLETS IN THE TEXAS ARMADILLO

In two species of the armadillo there occurs a form of polyembryony which is regarded by some as a modified type of twinning. The two species concerned are the Texas nine-banded armadillo, *Dasypus* (*Tatusia*) *novemcinctus*, and the South American Mulita, *D. hybridus*. The Texas armadillo typically produces four identical quadruplets from a single egg, while the

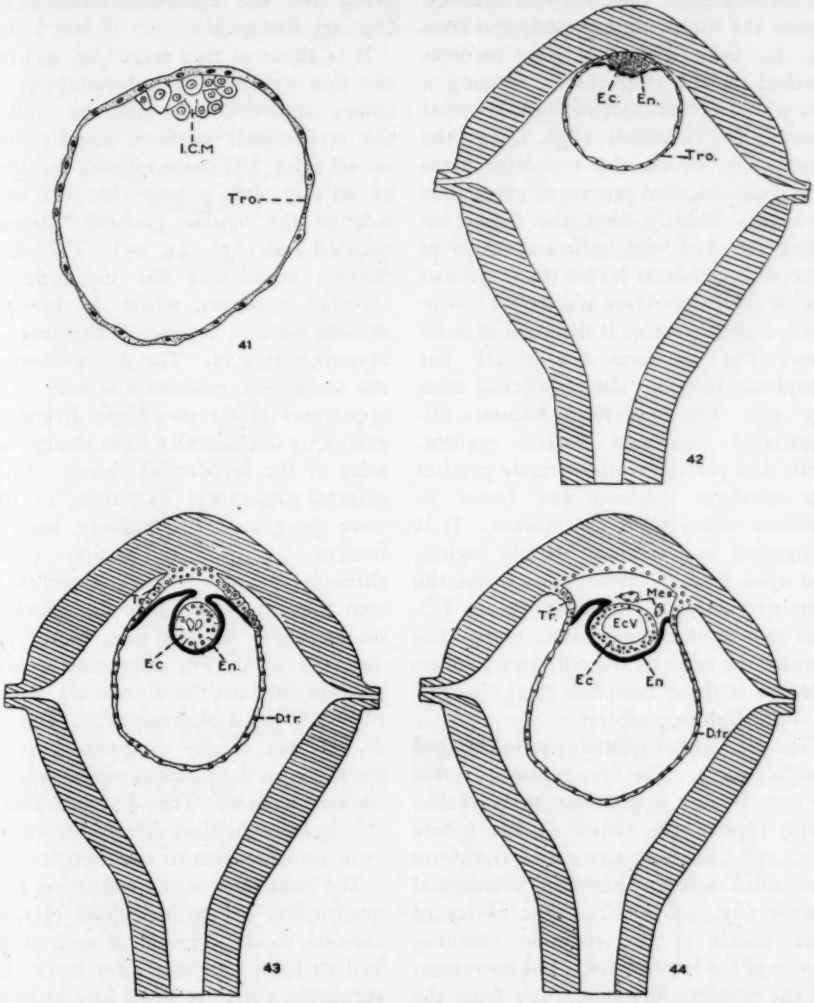
egg of Mulita gives rise to from seven to twelve individuals. In each species the several individuals arising from one egg are of the same sex.

H. von Ihering ('85, '86) was apparently the first to suspect that all of the young of one litter might be the product of one egg, for he had observed in each of two pregnant females that the eight embryos present were inclosed in a single chorion, and that all of the fetuses were of the same sex. However, the real discovery of polyembryony was not made until 1909. During that year two papers appeared in which it was shown that the several fetuses found in the pregnant uterus of each of the two armadillos are derived from one egg. Fernandez ('09), on the basis of his observations on several stages of Mulita, concluded that it was a case of polyembryony, and Newman and Patterson ('09) working on a few advanced stages of the Texas species, concluded that the four embryos must come from a single fertilized egg. Following this, a number of papers on the subject were published by Newman and Patterson, both in collaboration and separately, on the Texas armadillo, and by Fernandez on Mulita. As a result of these investigations it has been conclusively demonstrated that the mode of development is that of polyembryony, and that the process is practically identical in the two species. The following brief account is based chiefly on the conditions found in the Texas armadillos.

Unfortunately, the early cleavage stages of the armadillo ovum have never been secured for either species, but in the Texas species a series of developmental stages extending from late cleavage to full term, has been obtained and studied (Patterson, '13). The youngest ovum available has already passed through the so-called morula stage, and has become an embryonic vesicle or monodermic blastocyst. Such vesicles are usually found free in the cavity of the uterus, although a very few have been washed out of the fallopian tubes. We now know that the armadillo breeds sometime before the 15th of August, for a female of breeding age usually has a free vesicle in the uterus by that date. (For this datum I am indebted to Mr. G. W. D. Hamlett of this laboratory. Mr. Hamlett has made an extensive study of the breeding habits of the armadillo, and has secured a very large series of free vesicles and other early stages.) The remarkable fact is that the vesicle does not become permanently attached to the uterine mucosa for several weeks, or until sometime in October or November. A similar "period of quiescence" has also been reported for the blastocyst of the deer (Bischoff).

The young blastocyst of the armadillo is similar in practically every respect to that of many other mammals, and its structures give no evidence that it will produce four embryos instead of one. The blastocyst is composed of a typical trophoblastic layer, and the usual group of embryonic cells, or inner-cell mass (fig. 41). During the period in which the blastocyst is free in the uterine cavity, the inner-cell mass becomes differentiated into the two embryonic layers, the ectoderm and entoderm.

The didermic blastocyst then becomes attached to the mucosa at the tip of the fundus end of the uterus, on an area of the mucosa known as the attachment zone. The area of the trophoblast that forms the seat of attachment is the portion which directly overlies the embryonic ectoderm, and which is called Rauber's layer. Sometime before, the ovum, which is in the form of a flat, circular



FIGS. 41–44. FOUR STAGES IN THE DEVELOPMENT OF THE ARMADILLO BLASTOCYST

In figs. 42–46 the blastocyst is represented in a section, which is placed in a diagrammatic section of the uterus. In order to save space, the size of the diagram of the uterus is made much smaller in proportion to the size of the blastocyst. Fig. 41. A section of a very young blastocyst, showing the single layered trophoblast and the inner cell mass (I.C.M.). For a description of figs. 42–44, see text.

plate, becomes distinctly thicker (fig. 42), and after attachment it is gradually transformed into a spherical or ball-like mass.

The primary entoderm does not completely line the inner surface of the trophoblastic wall as in some mammals,

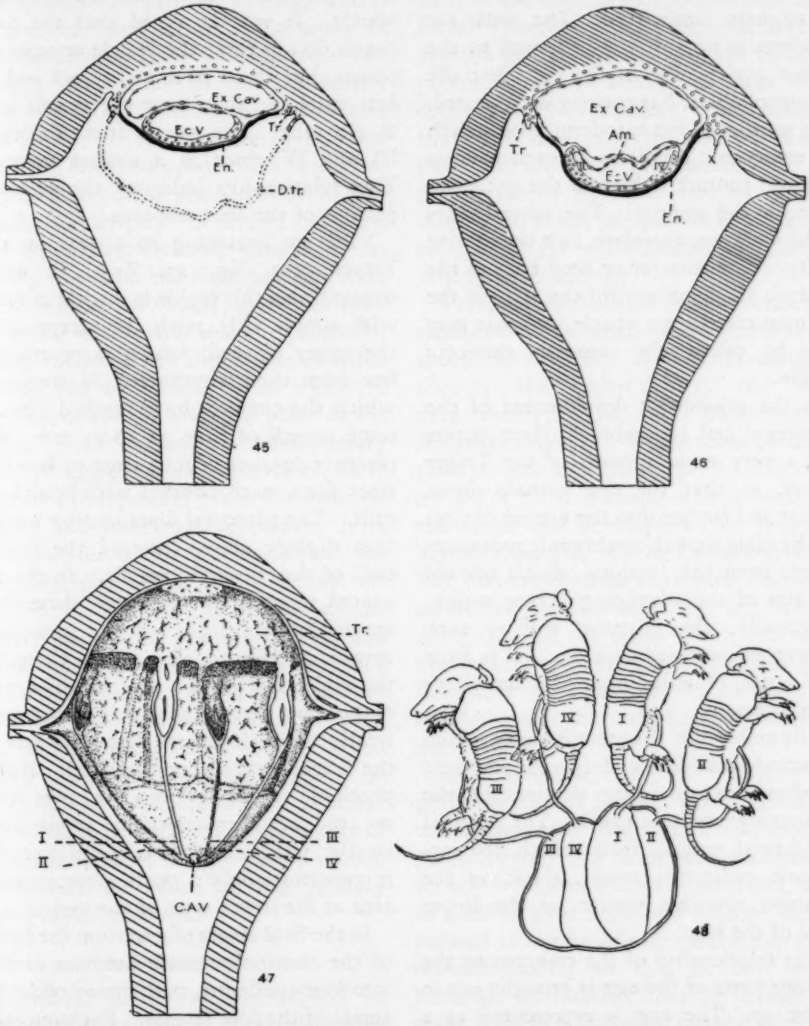
but its free edge ends a short distance beyond the limits of the ectodermal mass (fig. 42, *En*). This free edge becomes attached to the trophoblast, forming a zone which extends around the ectodermal sphere. The attached edge forms the pivot upon which the entoderm turns during the so-called process of germ-layer inversion. Shortly after the ovum becomes attached, the spherical mass of embryonic ectoderm leaves the inner surface of the trophoblast and moves downward, carrying before it the layer of entoderm. The entoderm finally all but completely envelops the ectodermal mass (fig. 43). The trophoblast becomes differentiated into two distinct regions. First, that portion which directly overlies the ectoderm thickens and forms an intimate union with the mucosa. It is recognized as the trophodermic region, and upon further development forms the primitive placenta, or Träger (fig. 43, *Tr*). The rest of the trophoblast, which lies beyond the edge of the entoderm, undergoes no striking morphological changes. It is the diplotrophoblast.

The ectodermal sphere is soon changed into a vesicle. The first evidence of this is seen in the appearance of vacuoles, lying toward the center of the sphere (fig. 43). These coalesce and transform the solid sphere into the ectodermal vesicle (fig. 44, *Ec.V.*). The cavity of this vesicle is the common amniotic cavity of the later stages. The movement of the ectodermal sphere away from the trophoderm creates a cavity between the sphere and the trophoderm. Groups of cells, apparently arising from the upper portions of the ectoderm, invade this space and soon form small vesicles. These constitute the beginning of the extra-embryonic mesoderm (fig. 44, *Mes*). The mesodermal vesicles fuse together and eventually form a complete living membrane for the extra-embryonic cavity (fig. 45, *Ex.Cav.*).

It is about at this stage (fig. 44) that the first evidence of polyembryony becomes apparent. At first the wall of the ectodermal vesicle is equally thick on all sides, but there follows a shifting of cells in such a way that the upper side of the vesicle gradually becomes thinned out (figs. 44, 45). This upper portion constitutes the true amniotic layer of ectoderm, while the lower or thicker portion represents the true embryonic ectoderm. The first evidence of the embryonic rudiments is seen in the appearance of the two blunt diverticula, extending out laterally from the opposite sides of the ectodermal vesicle. In the original publication (Patterson, '13) these were designated the primary buds. A median longitudinal section passing through the two primary diverticula is seen in figure 45. These diverticula lie on the right and left sides of the ectodermal vesicle. The embryonic ectoderm extends out into the diverticula as thick plates. The diplotrophoblast (fig. 45, *D. tr.*) has usually disappeared by this time, and in the figure is represented by a broken outline. The disappearance of the diplotrophoblast directly exposes the yolk sac entoderm to the uterine cavity.

The next step in the formation of the quadruplets in the armadillo blastocyst consists in the division of each primary bud to form two secondary buds. Consequently, there are in all four embryonic rudiments. The secondary diverticula arise in each primary as two thickenings in its wall. One of these is situated at the extreme tip of the primary bud, while the other appears slightly to the left (as viewed from the yolk-sac of each of the blastocysts). The Roman numerals I to IV, are used to designate the four primordia thus produced. The embryos

are, therefore, grouped in two pairs, Nos. I and II constituting one pair and Nos. III and IV the other pair. To distinguish this fundamental arrangement of the embryos from that of their final position in the uterus we shall refer to it as the primary pairing.



FIGS. 45–48. See text for description of figs. 45–46. In fig. 47 the entire blastocyst is shown in the diagram of the uterus. The relative sizes of uterus and blastocyst are approximately that of normal. Fig. 48 shows uterus split open and the four half-grown fetuses spread out in such a way as to reveal their paired arrangement.

In figure 46 is shown a section passing through the embryonic rudiments II and IV. The diverticula of these two embryos

extend out laterally from the right (IV) and left (II) sides of the original ectodermal vesicle (*Ec. V.*), from which they are slightly constricted. The yolk sac entoderm is now directly exposed to the uterine cavity, due to the fact that the diplotrophoblast has entirely disappeared. That portion of the entoderm upon which the embryonic ectoderm of each embryo comes in contact will form the gut entoderm for the embryo. The ventral sides of the embryos, therefore, face the uterine cavity. The anterior or head ends of the embryos all point toward the apex of the common ectodermic vesicle, or what may now be called the common amniotic vesicle.

In the subsequent development of the blastocyst and its embryos, there occurs first a very rapid growth of the Träger region, so that the egg extends down farther and farther into the uterine cavity. At the same time the embryonic rudiments retreat from the amniotic vesicle toward the rim of the advancing Träger region. Eventually, the posterior end of each embryo unites with this rim. It is from this point of union that the umbilicus later arises.

The embryo in thus moving away from the ectodermal vesicle, draws the amniotic ectoderm out into a long, slender tube, the connecting amniotic canal. The original ectodermal vesicle, from which the embryonic rudiments arose, is left, as the common amniotic vesicle, at the lower apex of the egg.

The relationship of the embryos to the various parts of the egg is brought out in figure 47. The egg is represented as a semi-transparent object, placed in a diagrammatic section of the uterus. Each embryo has reached the primitive streak stage, and has its anterior or head end directed toward the common amniotic vesicle, with which it is connected by a canal. Its posterior end is united with the rim of the Träger. The four connecting canals converge toward the amniotic vesicle. It will be noted that the four canals do not enter the vesicle at separate points, but those from embryos I and II first unite and then enter the vesicle as a single tube. The canals from Embryos III and IV enter in a similar manner. This relationship indicates the primary pairing of the four embryos.

Villi are beginning to appear on the Träger area (fig. 47, *Tr.*). In early somite stages this region is thickly covered with simple villi, with the exception of the upper tip end, which is practically free from these structures. In stages in which the embryos have reached a head-rump length of from 12 to 15 mm., the placenta consists of four more or less distinct discs, each covered with branching villi. The placental discs occupy a position slightly above (toward the fundus end) of the chorionic vesicle. In the advanced stages of development, these discs are distinctly paired, one pair occupying approximately the left side and the other the right side of the vesicle. The villi of the upper part of the vesicle remain practically undeveloped, so that this area of the Träger becomes non-placental. As the chorionic vesicle develops, its lower yolk-sac end becomes relatively smaller and smaller, until in the late stages of gestation it constitutes only a small, clear, cap-like area at the lower apex of the vesicle.

In the final stages of gestation the cavity of the chorionic vesicle becomes divided into four quadrants, partitioned off by the amnia of the four fetuses. Each quadrant contains a fetus and its umbilicus. The arrangement is such that embryo No. I occupies the ventral quadrant and its paired mate (II) the left quadrant, while embryo No. III occupies the dorsal quadrant and its mate (IV) the right quadrant.

This arrangement clearly constitutes a secondary pairing, which may or may not correspond to the primary pairing, for it is possible to demonstrate, by a study of early budding stages, that the four embryonic diverticula do not necessarily show the same relation to the uterine axes as do the four fetuses of the late stages. (The facts upon which this statement is based are contained in an unpublished manuscript.) In certain cases the two primary diverticula, instead of extending out from the right and left sides of the ectodermal vesicle, grow out from the dorsal and ventral sides, respectively. Hence, the secondary diverticula of either primary bud will extend to the right and left sides of the dorsoventral plane of the uterus. Since all traces of the primary pairing disappear at a comparatively early stage of development, when the common amnion and its canals degenerate, it is never possible to tell whether or not the secondary pairing is the same as the primary. It may well be that when the primary buds arise from the dorsal and ventral sides of the vesicle embryos I and IV will constitute one of the secondary pairs, and Nos. II and III the other pair. The lateral arrangement of the paired discoid placentae, lying as they do on the right and left sides of the chorionic vesicle, must be regarded as the result of the bilateral blood supply of the uterus, rather than the result of the primary pairing of the embryos.

6. DISCUSSION

A general survey of the subject of polyembryony makes it clear that this type of development has arisen independently in several different groups of animals, and in some of these groups has undergone a distinct evolution. Since polyembryony has thus arisen and evolved it is not to be expected that its exact mode of expression would be the same in each of the several groups in which it is found. For this reason, any attempt to apply a general theory as to the cause of polyembryony is certain to meet with difficulties. Nevertheless, it is possible that in the final analysis it will be found that the causal factors underlying the production of multiple embryos are the same in all cases, irrespective of the exact mode of origin or the number of embryos arising from the egg.

Various theories have been advanced to explain the occurrence of polyembryony, such, for example, as the "blastotomy theory," the "fission theory," the "budding theory," and the "physiological isolation theory." While some of these theories may have merit, yet I think that no one of them is adequate to account for the origin and development of polyembryony among the different animal groups. The various theories have been discussed rather fully by Newman ('17, '23), Stockard ('21), and the writer ('13), and need not be reviewed in this brief discussion. Instead, I shall consider certain facts of polyembryony that may bear on the question of theory.

In discussions on the subject of polyembryony it has not been customary to emphasize the obvious fact that specific polyembryony is a developmental characteristic which is definitely inherited, and as such it must arise and become incorporated in the hereditary mechanism in a manner similar to that of any other heritable character. That is to say, it must arise as a variation having survival value, and hence effective in adaptation. Specific polyembryony can be interpreted as a form of adaptation, for the reason that it results in an increase in the number of offspring from the egg. This might

have the effect of increasing the chances of survival of any species having this type of development.

There is considerable evidence to show that polyembryonic development has undergone a very distinct evolution within certain groups, *e.g.*, the parasitic Hymenoptera. In the Hymenoptera it is possible to arrange a series in which polyembryony begins as a simple type of twinning, and gradually increases in complexity until in some species more than a thousand individuals are produced from one egg. Moreover, it is possible to trace throughout this series the several steps by which this complexity has taken place.

The same is probably true for the armadillos, although the evidence is less complete. The facts on the development of armadillos are still fragmentary, but such as we have clearly indicate that the armadillos were formerly multiparous, and then gradually evolved to a condition of uniparity. In the living species the uterus is of the simplex type, somewhat like that of the human. Nevertheless, some of the non-polyembryonic species still show a strong tendency to ovulate and gestate two eggs. Some few species, however, are said to be entirely uniparous. It is from this condition that polyembryony has evolved; first by the production of identical twins (probably), then by the formation of quadruplets, and finally by the production of from eight to twelve embryos from the egg.

Another point of significance is the fact that before specific polyembryony is established in a given group of organisms the monembryonic type of development in the group often has become highly specialized, and it is probably true that without such specialization polyembryony would not become established as the exclusive mode of development.

This review has been devoted almost entirely to cases of specific polyembryony, but in conclusion it seems desirable to make a suggestion concerning what has been termed sporadic polyembryony. Such cases occur throughout the entire animal kingdom, although their appearance in any given species may be very rare. In some species sporadic polyembryony gives every evidence of being hereditary. Thus in the case of human identical twins several writers have pointed out that such twinning must be inherited, because of the fact that it appears with very great frequency in certain families (see Davenport, '20). However, most cases of sporadic polyembryony give no evidence that heredity is involved. From reading the reports on such cases, one gains the conviction that their occurrence is the result of "environmental accidents," such as the separation of the early blastomeres. I would suggest that the results obtained in experimental polyembryony offer an explanation of the cause of such sporadic cases rather than that of specific polyembryony.

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ABNORMAL SEXUALITY IN ANIMALS

III. SEX REVERSAL

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IT IS somewhat difficult, when one first approaches this subject of the transformation of sex, to grant that reversal is possible in the higher forms in which the sexual differences, morphological, physiological, and mental, are so sharply emphasized. But when one remembers that what is rare and exceptional in one form can be facultative in others, and that all forms have much in common, the difficulty vanishes. It is readily conceded that the oyster, for example, may regularly change its sex. The native oyster begins its life as a male and then, when one or two years old, may and indeed commonly does become a female. But that is not all, for Orton (1921) has shown that such an oyster, after becoming "white sick," *i.e.*, after shedding its ova into the mantle cavity, and whilst still carrying its own embryos, can, within the space of a month, become equipped as a male once more. That which is usual in the oyster may be under certain conditions not rare in the more highly organised forms. Similar instances of facultative sex-transformation are those furnished by *Crepidula plana* (Conklin, 1898; Orton, 1909; Gould, 1917), parasitized Cymotheids and Epicarids (Mayer, 1879; Caullery, 1908; Bonnier, 1900; Smith, 1906), *Asterina gibbosa* (Cuénot, 1898; Harms, 1926), and *Limax maximus* (Baber, 1894). In all these cases the direction of the transformation is ♂–☿–♀.

The sex of an individual of a bisexual species is said to have been completely reversed when the individual has assumed the sex-characterization typical of one with the alternative sex-chromosome constitution. Thus sex-reversal of a female implies that a genotypic female (XX) loses her typically female sex-characterization and develops that type of sex-equipment which is essential for the elaboration of functional spermatozoa and for the efficient conveyance of these to the site of fertilization.

The recorded instances of this phenomenon occurring in species in which it is to be regarded as abnormal can be classified for purposes of discussion according to the following scheme.

A. Sex-reversal can be the direct expression of genetic action

If the genetic components of sex-reversal are present in the genotype of an individual, if the physiological equilibrium of the zygote established by the action of the genotype (the sum total of all the genes) is not profoundly modified by the physiological influence of the glands of internal secretion during development, and if the impress of external agencies upon the zygotes does not or cannot override the genotype, *i.e.*, does not or cannot profoundly alter the physiological state established by the genotype, then sex-transformation will occur as development and differentiation proceed.

Thus in the case of the moth, *Lymantria*, and similarly constituted forms, the forces which lead to intersexuality lead also to sex-reversal. Intersexuality is in such cases merely incomplete reversal. Complete reversal will occur when in a genotypic male the quantitative disharmony between the male and the female sex-differentiating reactions is such that the female reactions are in excess throughout the whole of the period of differentiation, or in the case of a genotypic female when the male reactions are in efficient excess throughout this time.

In the Lepidoptera Goldschmidt (1920, 1923), Harrison (1919), and others, have obtained species hybrid broods that were largely or entirely of one sex. Harrison was able to show that in one of his cases the mortality was not sufficiently high to account for the results obtained; it was not a case of a sexually selective prenatal mortality, and both Goldschmidt and Harrison have presented evidence which strongly indicates that the results are due to a sex-transformation of half the individuals concerned. Unisexual broods in these forms are to be regarded as the final stage of intersexuality. Sturtevant (1920) records similar unisexual broods in *Drosophila melanogaster* × *D. simulans* crosses, but finds that the cause of this is a selective mortality.

Another instance of direct genetic sex-reversal would seem to be that of the fish *Xiphophorus*. Essenberg (1925) records that sex-reversal occurs in the viviparous teleost fish, *Xiphophorus helleri*, (the sword-tailed minnow), and that many instances of this have been reported by fish breeders and fanciers. In Essenberg's cases two females ceased to produce young when about three years old, and during the course of several weeks took on the sex-characters of the male. Cytological examination revealed the presence of ripe sperm in all parts of the gonad which, however, was juvenile in relation to the size and age of the fish. Essenberg was able to show that there is a type of development in the female which readily provides a morphological basis for the change-over. He also shows that there is a complete reversal of the sex-ratio in a population, this being 50:100 among immature fish and 100:50 among mature, a fact which supports the suggestion of sex-transformation of 50 per cent of the females. In many males, moreover, the shape of the testes closely resembles that of the ovaries, and the grades suggest a transformation of pre-existing ovary into testis. It would seem from Essenberg's observations that sex-reversal is extremely common in this fish and that it is genetic in origin, there being a form which through genetic action is destined merely to pass through a female phase and later to proceed to a male type of sex-differentiation. The case is very similar to that of *Lymantria*, save that even in a well grown individual a remodelling of the sex-organization can take place, there being no permanent hard parts.

Harms (1926) also has observed the transformation of females of *Xiphophorus* into males at different ages, especially among old sterile females. He records that during this process of sex-reversal the female when mated still produces young, though when the process is completed, the individual is a functional male, larger than the normal male, broader and heavier. Harms observed that the older the animal is at the time of the change-over, the more female the general body build remains. The process occupies about 3–4 months and in the case of old females it may remain incomplete. The cause of the transformation is regarded by Harms as being a physiological exhaustion of the ovary with a consequent alteration

in the general metabolism which invokes the differentiation of testicular tissue. He thinks that inbreeding favors sex-transformation.

Harms bred from his transformed females when they were functioning as males and got none but females, as would be expected if the female of the fish is monogametic and if sex-reversal does not affect the nature and distribution of the elements of the sex-chromosome sex-determining mechanism.

Other cases of what would seem to be sex-reversal in fishes have been recorded by Herzenstein (quoted by Essenberg) in the cyprinodonts *Cymnocipris potanini* and *Schizopygopsis güntheri*, in which cases also females assumed the sexual characters of the male. Philippi (1904) reported a similar case in the viviparous teleost, *Glaridichthys caudimaculatus*, and three others in *Glaridichthys januarius*, while Newman (1908) described a case of hermaphroditism in *Fundulus majalis* which would seem to be one of sex-reversal. Winge (1927) describes certain cases of intersexuality in *Lebistes reticulatus* which may possibly be of this nature. The changes occurred in old females which though still functioning as females assumed certain of the male sex-characters.

A very considerable number of cases of hermaphroditism in different species of fish have been recorded. It is unfortunate that in the majority of these the description is inadequate; however, the indications described are either stages in sex-reversal or are cases of intersexuality similar to those occurring in the mammal. That certain of them are indications of a sex-reversal probably exactly similar to that in the case of *Lymantria* is very probable. In addition to the case of *Xiphophorus* there is the suggestive one of *Girardinus poeciloides*, the "millions" fish, examined by Huxley (1920). Boulenger had reported that the sex-ratio of a stock bred in the London Zoological Gardens was three females to one male for a period of nine to ten months, that this had then given place to a sex-ratio of one female to two males, and lastly to one of equality. Huxley suggests that this swing in the sex-ratio is due to the fact that some of the females of the population in which the sex-ratio was three females to one male were genotypic males which had undergone sex-reversal to become phenotypic (or somatic, as Shull, 1914, would call them) females. These phenotypic females, still XY in sex-chromosome constitution, would elaborate two sorts of eggs, in respect of the elements of the sex-determining mechanism, instead of one, and these being fertilized by X- and Y-bearing sperm would yield in every three on the average one female (XX) to two males (XY), the YY zygote being non-viable. If this sex-reversal had affected a certain proportion of the males of one generation, then two out of every three females would be normal in the next, so that the sex-ratio would swing back to five females to six males. If sex-reversal continued for several generations there would ultimately be a swing in the opposite direction to give a preponderance of males.

Langerhans (1876), Goodrich (1912), and Orton (1914), have recorded cases of intersexuality in *Amphioxus*. Orton's specimen was 4.4 cms. long and was predominantly male; only one of the forty-three gonad pouches contained ova, the rest being filled with sperm. The digestive gland was also abnormal. Orton suggests that these cases are but stages in a process of sex-transformation in the direction male-female. These intersexual specimens were of medium size.

It will be noted that the interpretation offered later on to explain sex-transformation in the fowl suggests that in the bird

also the genetic components of sex-reversal are present in every hen. In effect, it is suggested that every hen would inevitably become a cock but for the fact that within her body there is an ovary, a legacy from the phase of her development when the valency of the female determining reactions was greater than that of the male reactions. It is the physiological influence of the ovary which prevents the expression of the genotype: if the ovary is removed, then an internal environment of maleness, the direct expression of the genotype after embryonic life, becomes established, and a male characterization is assumed. But since the ovary remains in the "normal" hen, sex-reversal is abnormal; it occurs only when the genotype is unbolted by the removal of the ovary. For reasons of convenience, the case of the fowl is not included in this category to which indeed it would seem to belong.

B. Sex-reversal can be the result of the overriding of the genotype by agencies which sufficiently disturb the general physiological conditions of the zygote at some stage or other of its development

1. It can result from a disturbance of the physiological condition within the ovum before fertilization. The work of Hertwig (1906, 1912), of Kushakevitch (1910), and of Witschi (1914), has shown that delayed fertilization and also the exposure of the eggs before fertilization to high temperature (27°C.) leads to a profound disturbance of the sex-ratio among the offspring. The male frog was permitted to fertilize half the eggs of a female and then was removed, to be replaced after an interval to fertilize the remaining eggs. After an interval of 89 hours none but male offspring were obtained. It was established that this result was not due to selective fertilization, to a sexually selective mortality among the embryos, or to the abnormal extrusion of the X-chromosome during the maturation of the ova. The correct interpretation of the results would seem to be that some 50 per cent of the eggs were fertilized by X-chromosome-bearing spermatozoa, genotypic females (XX) being produced, but that the conditions of the experimentation were such as to transform these into phenotypic males, the sex-chromosome constitution of the zygote being overriden by the effects of delayed fertilization upon the metabolism of the egg. The results obtained by Mršić on the effect of overripeness upon the egg of the trout are probably to be explained in a similar fashion.

King (1912) has shown that desiccation of the toad's egg yields exactly opposite results, for she obtained 87 per cent of females in an experiment in which the mortality among individuals of unknown sex was less than 7 per cent. In the case of the frog, Witschi (1914) not only obtained individuals which were instances of complete sex-reversal but got in addition numerous intersexual forms of various grades.

The observations of Adler (1920), who has shown that the thyroids of individuals from these late fertilized eggs are markedly hypertrophied, would seem to be of significance. Adler suggests that in these individuals the thyroid comes into action earlier than does the gonad and so affects the internal environment that the gonads, when they do differentiate, become testes.

These observations are closely in line with those of Whitman (1919) and of Riddle (1912, 1916) upon the pigeon. It was found by Whitman that the matings of birds belonging to the Columbidae and of two widely different zoological families resulted in the production of male offspring only, and that female offspring alone were obtained from the eggs of

doves which had been forced to lay excessively and at an abnormally rapid rate. Riddle carried these observations further and was able to show that the eggs that yield males can be distinguished from those which yield females, that maleness is associated with eggs of smaller size, higher water content, and less stored energy, and that the production of all males or of all females was associated with the production of eggs of one or of the other type. He was able to dismiss the possibility of selective fertilization and of differential maturation, and was driven, against his will it would seem, to the conclusion that the conditions of the experiments were such as to induce sex-reversal in the egg itself (1914, 1919).

It is a simple matter to interpret these results in terms of a metabolic theory of sex as elaborated by Riddle. Delayed fertilization implies an increased metabolic rate in the egg and a high metabolic rate implies maleness. Desiccation implies a decreased metabolic rate and femaleness. The hypertrophy of the thyroid implies an increased metabolism and an internal environment of maleness. The production of offspring all of one sex by matings of wide crosses is to be interpreted as the result of the pooling of genes which in their action lead to the establishment of one kind or the other of metabolic level in the zygote. Castle (1926) discussing the general question of hybrid vigor argues that the zygote is not a mere summation of the factors contained in the two gametes but that the hybrid state itself is a source of metabolic energy in the zygote. There seems, however, no real difficulty in assuming that the ultimate source of metabolic energy is the genotype.

In this connection it is of interest to note that Guyer (1909) has collected data on species hybrids among certain birds and has shown that there is a decided excess of males in the F_1 generation. The cause of this has not been demonstrated. Riddle (1916) recorded an excess of females in the cross *Streptopelia risoria* × *S. alba* (doves) under certain conditions and concluded that this excess was the result of a transformation of some of the males. It has been shown, however, that this conclusion is not justified, for the cross involved a sex-linked character and of the hybrids the males are dark, the females white in color, and examination of the data for sex and also for color shows that the only possible explanation of the excess of females is that which postulates that the conditions of the experiment were such as to cause the X-chromosome to pass into a polar body at the time of the reduction divisions more often than to remain in the egg.

Riddle (1912, 1914, 1916, 1917) has shown that a higher metabolic rate is associated with maleness and a lower rate with femaleness. He has shown that in the case of his pigeons the season of the highest male production is the winter and that is the season when the thyroid of the pigeon is largest and when there is least storage of energy within the ova, as estimated by burning the yolk in a bomb calorimeter; and conversely that the period of the greatest energy of fat storage and of the smallest thyroid size is the period of the greatest excess of females, and he argues that the facts concerning the type of metabolism induced by the different kinds of experimentation all point to the conclusion that the causal agent in sex-transformation is the establishment of that type of metabolism which is characteristic of the alternative sex. It may be that many of the peculiar phenomena associated with parthenogenesis, particularly those which concern the effect upon the sexuality of the egg of environmental

agencies (Maupas, 1891; Banta and Brown, 1924) are to be explained in a fashion somewhat similar to the above.

2. *It can result from a disturbance of the general physiology of the individual during embryonic life.* It is possible, but not probable, that those agencies which commonly lead to the production of a freemartin in cattle and goats occasionally result in the production of a completely transformed individual (Lillie, 1923; Bissonette, 1924). This, however, must yet awhile remain pure speculation.

Burns (1925) joined young embryos of *Amblystoma* in the tailbud stage in parabiosis and instead of getting the expected chance combinations of the sexes, 1 ♂♂, 1 ♂♀, 1♀♂, 1 ♀♀, he obtained exclusively one sexed pairs. He suggested that the reason for this 44 ♂♂ : 36 ♀♀ or 1:1 ratio was that in one-half of the original ♂♀ and ♀♂ associations the males became transformed into females, whereas in the other half the females became transformed into males.

Witschi (1927), using four different species of frogs, joined embryos 50–70 hours old, and shortly after the closure of the medullary tube, in parabiosis. The controls exhibited the first signs of sex-differentiation during the third week of development; in the case of the parabiotic twins it was somewhat delayed. The twins were preserved at intervals during the larval period and the stage of metamorphosis. The sex-ratio among the controls was 96 ♂♂ : 100 ♀♀ or 1:1. Among the 56 twins there would be expected the following sex-combinations: 14 ♂♂, 14 ♂♀, 14 ♀♂, 14 ♀♀. There was found on examination 16 ♂♂, 17 ♂♀ (with 7 of the ♀♀ exhibiting some stage in sex-reversal), 10 ♀♂ (with 4 of the ♀♀ undergoing sex-reversal), 13 ♀♀. The combination of a female with a male twin undergoing sex-reversal was not encountered. Witschi therefore concluded, unlike Burns, that the male sex-differentiating agencies predominated and that sex-reversal did not take place before the time of sex-differentiation since 29 one-sexed and 27 two-sexed pairs is as near as possible to the expected 28 ± 2.5 and among the individuals there were 59 ♂♂ and 53 ♀♀, the deviation from the mean being less than the single P.E.

Disharmonies in the time relationship during development when the stimulus to sex-differentiation is exhibited may provide opportunity for sex-reversal. For example, in *Myxine* (Schreiner, 1904), growth would seem to proceed undirected to the stage when the individual is hermaphroditic, before the processes of sex-differentiation set in to convert the individual either into a functional male or else into a functional female. In the young males of *Perla marginata* both ovarian and testicular tissues are to be found but the ovarian tissue undergoes atrophy, so that in the adult none but testicular remains (Junker, 1923). In such circumstances as these the morphological basis of a possible sex-reversal is revealed and it becomes entirely conceivable how physiological disturbances during embryonic and early post-embryonic life can change the course of differentiation and lead to the conversion of a genetic male into a functional female, and *vice versa*.

In his interpretation of the bovine freemartin, a female rendered abnormal in respect of her sex-organization by the action of the physiological influence of the testes of the male co-twin *in utero* which enters her body by way of a vascular anastomosis, Lillie rejects the idea of the dominance of the male sex-differentiating reactions in favor of a time relation in the production of male and female hormones, that of the testis, as suggested by the work of Chapin (1917) and of Bascom

(1923), being elaborated earlier in development. Lillie, however, freely admits that other causes may also exist. In the case of the parabiotic twins of frogs the time factor does not enter, for there is a physical basis for a definite antagonism between male and female differentiators. The male differentiating reactions first embarrass and then suppress the female.

Doncaster (1920) suggested that the occasional tortoiseshell male cat was a sex-reversal female produced in the same way as is the free-martin in cattle. He, and later Bamber (1922), examined a considerable number of pregnant uteri of cats and found no instance of a confluence of blood vessels. Bamber (1922) puts forward the suggestion that the tortoiseshell male is indeed a transformed female or *vice versa*, but that the reversal is not the result of the intra-uterine action of the sex-hormone of a male co-twin but of a metabolic change in the egg similar to that described by Riddle in the case of his pigeons. In a later paper (1927) however, she exhibits a preference for another interpretation.

3. It can result from a disturbance of the general physiology of the post-embryonic individual. The conditions necessary for such sex-transformation are (1) there must be a switch-over from one type of metabolism to the other, from the female to the male, or *vice versa;* (2) the component structures of the sex-equipment must be capable of transformation or replacement, one kind of gonadic tissue must be replaced by the other, ovary must become or be replaced by testis, or *vice versa*, the accessory sexual apparatus, the external organ of reproduction, the rest of the secondary gonadic characters must be remodelled or replaced.

Complete sex-reversal therefore cannot occur in any individual or form in which the internal and external genitalia, being fashioned early in embryonic life, thereafter lose their plasticity and become unresponsive to any stimulus which, had it been exhibited at the time of their differentiation, would have controlled these processes. Nor can it occur in those cases in which the differences between male and female sex-equipments are based upon the differential development of two different sets of structures one of which, in either sex, undergoes complete atrophy. No more can it take place in those forms in which sex-dimorphism involves a differential mode of development of one and the same set of structures, for if one plan of differentiation is pursued, the steps cannot be retraced and the alternative route then followed.

Harms (1923) and Guyénot and Ponse (1923, 1925) have shown that if young castrated male toads are fed on a diet containing an excess of fat, lipoids, and lecithin for a considerable period of time, the caudal portion of Bidder's organ becomes differentiated as an ovary and the cephalic portion as a new organ of Bidder, and that oviducts and uteri are developed while the pointed head becomes transformed into the blunted characteristic of the female. Ponse (1925) succeeded in rearing 9 metamorphosed offspring of one such transformed male functioning as a female and of these 6 were males and 3 females. Harms raised 184 such offspring and of the 161 the sex of which could be identified there were 104 males and 57 females. If in the toad the male is digametic, and if the YY zygote is non-viable, the expected sex-ratio is 2 ♂♂ : 1 ♀.

In this connection reference must be made to the work of Russo (1911), who recorded that in the rabbit there are two kinds of fertilized ova, one containing lecithin and the other crystals of fatty acid. He suggested that the lecithin-containing ova are anabolic (female),

the others catabolic (male). The experiments of Russo (1909) in which he endeavored to affect the sex-ratio by administering lecithin have been subjected to severe criticism by Basile (1908), Punnett (1909), and Castle (1910). However, there would still seem to be reason for holding that Russo's work should again be repeated.

Champy (1921) records that when a male triton (*T. alpestris* Laur.) was fed intensively after the winter's starvation, he assumed the external characters of a female, and that within the pre-existing testicular tissue there were to be found immature but unquestionable ova. He had previously shown that the annual process of spermatogenesis in tritons could be inhibited by starvation and that in the absence of spermatogenesis there was no development of the external sexual characters, the animal exhibiting the "neuter" state corresponding to that of the male in winter. In this "neuter" state there are to be found in the testes primitive gonocytes and spermatogonia. In animals killed in the spring, following starvation, the testis was represented by a longitudinal strip of fat. Two of these starved "neuter" tritons, when fed intensively, lost the dark blue even coloration of the back and assumed a greenish shade mottled with distinct blue marks, as in the female, whilst the yellow dorsal line became more and more attenuated. One of these animals was killed in January and there was found the expected strip of fat with a few spermatogonia. The other was kept alive and in February was exactly like a female in appearance. It was kept until April when post-mortem examination revealed within each of the strips of fat an elongated organ of granular appearance resembling an ovary, together with an oviduct.

Histologically this organ was an immature ovary. Champy points out how this case exemplifies the ambivalency of the primitive gonocytes for these, instead of becoming sperm, became differentiated into ova.

Zavadovsky (1922), Bénoit (1924), Domm (1924), and Finlay (1925) have each shown that following the removal of the left gonad of young female chicks there is developed in the right gonadic site a testis and the bird assumes the characterization of the male. Caridroit (1925) has shown that if the ovary of the fowl is displaced or if ovarian tissue is implanted, ovarian tissue is replaced by testicular.

In addition to these experimental studies in sex-reversal, the following cases have been observed. In the case of one of the frogs resulting from the "egg-overripeness" experiments, Witschi (1923) was able to show that indeed it was a transformed female, for when mated with a normal female it sired only female offspring. This is as would be expected, if in its fundamental chromosome constitution it still remained XX, for then all its spermatozoa would be X-chromosome-bearing and on fertilizing X-bearing eggs would yield none but XX zygotes. Crew (1921) had previously encountered a similar case in the frog. It was a male used for breeding and when post-mortemed was found to be a "hermaphrodite" with degenerate ovaries and functional testes. Among its offspring were none but female. Witschi (1921) was able to show that in the case of another hermaphroditic frog both functional ova and sperm, all X-chromosome-bearing, were produced.

Riddle during the years 1914–1918 had observed the first case of complete sex-reversal in the adult bird, but he did not publish an account of this case until 1924. A ring-dove (*Streptopelia risoria*) laid eleven eggs at times exactly observed between 27th January and 15th April, 1914.

During the six months following she and a male mated three times, began sitting on a nest without producing eggs, and raised young of other parents. During the following nineteen months her sex-behavior and mode of growing changed to that of a male, frequently forcing her male mate to act as a female in copulation. At twenty-two and a half months after producing her last egg, this bird and mate were transferred to a pen with a few other spent inactive doves. The male of this pair died three and a half months later, and weights and dimensions of testes were obtained. Twenty-one months after transfer, the bird died, showing very advanced abdominal tuberculosis. Two testes were found, removed, and weighed. If any residue of the original ovary remained it was wholly included in a tuberculous mass, involving spleen and liver. At the time of autopsy this bird was supposed to be the original male of the pair, and therefore the testes were not saved for demonstration. The bird had lived forty-four and a half months after producing the last egg, became tuberculous, assumed male behavior, the curve for the body weight during the three years undergoing a remarkable change, and at death it possessed two unmistakable testes. Riddle interprets this transformation as the result of the increased metabolism which followed the destruction of the ovarian tissue and the presence of tuberculosis.

Crew (1923) described the case of a Buff Orpington hen, the reputed mother of many chickens, which when three years old was attacked by tuberculosis and developed male characters, to become a fecund male and the father of two chickens. Post-mortem examination revealed the presence of two functional testes and a highly degenerate mass of ovarian tissue destroyed by tubercular disease. This case alone could not be regarded as providing conclusive proof of sex-reversal in the fowl, for during the earlier part of its life this bird had been in the possession of a private breeder concerning whose integrity there is no doubt but whose powers of critical observation can, of course, be held up to question. However, Crew (1923) and Fell (1923) examined a series of sexually abnormal fowls and were able to demonstrate that the condition found in these could logically be interpreted as stages in the process of transformation from a female type of sex-organization to a complete male type. Similar cases have been described by Bronté Gatenby (1924) and Parkes and Brambell (1926).

More recently, the writer has examined three fowls which have been in his possession for two years or more. These were sent to him by private breeders as "hens which had become cocks." One of them was a carefully trapnested and legbanded White Leghorn hen which, it was stated, had laid 111 eggs in her second year. Each of these birds when received was imperfectly male as far as the plumage characterization was concerned, far more like a hen than a cock in shape, stance and length of long bones. Each rapidly assumed the complete male plumage and sexual behavior. They were tested for fertility and proved to be fecund when mated with normal hens. Efforts were made to raise a great number of chickens from these pens in order to examine the sex-ratio of the offspring, but, since the numbers were small and infertility common, it was not found to be practicable to raise a sufficient number. By the application of the Manoilov test to these birds an intermediate reaction was obtained which approached the female much more closely than the male. Post-mortem examination revealed a perfect male sex-equipment, no sign of ovary or of oviduct being found.

(Naturally, therefore, the accounts of the private breeders who had sent in these birds were queried, but they insist that their observations and statements are authentic.) It is possible that certain of these birds were nothing but late maturing cocks but one cannot refuse to consider the possibility that complete sex-reversal in the fowl does occur fairly commonly and that when such a bird is finally examined no morphological evidence of persisting ovary and oviduct will be found. An appeal to cytological differences between male and female does not help, and as yet the biochemical identification of sex is not sufficiently delicate.

In the mammal complete sex-reversal cannot occur in post-embryonic life, because of the differential mode of development of the internal and external genitalia. If urogenital cleft and genital tubercle become scrotum and penis, these cannot become dedifferentiated and develop anew into vulva and clitoris. If the Wolffian duct derivatives proceed to full differentiation and those of the Müllerian ducts undergo atrophy there cannot later be a reversal of these processes.

A consideration of these instances of sex-reversal will show that in the egg stage and in the post-embryonic stage of Amphibia and in the case of fish also, if Huxley's interpretation of Boulenger's results is correct, reversal can occur in either direction, female to male, and *vice versa*, whereas in the post-embryonic stage of birds it has thus far been demonstrated in one direction only, from the digametic sex to the monogametic. In this connection it is of interest to note that in the instances of intersexuality in *Lebistes* observed by Winge (1927) the change occurred in old females which assumed male characters though still breeding as normal females. That this is so is provocative of thought. It is possible that the balance between male and female sex-differentiating reactions is more easily disturbed in the case of the sex which possesses but a single X-chromosome, a suggestion which is in line with the observation of Haldane (1921) that in the case of specific and wide varietal crosses if among the offspring one sex is absent, rare, or sterile, that sex is the digametic.

In the case of Amphibia, fishes, and birds, the conditions required for complete sex-reversal are readily met. In the Amphibians and birds it has been shown that it is possible experimentally to masculinize a female and to feminize a male by appropriate gonad implantation. Male and female accessory sexual apparatuses and external genitalia are very similar, the sexual differences commonly being nothing more than differences in the degree of development of common structures, or, in the case of such as are developed from different rudiments, the set appropriate to the alternative sex becoming completely atrophied. All that is required is that one kind of gonadic tissue shall be replaced by the alternative kind. In the case of the Amphibia if, as seems the case, at the end of the breeding season the gonads are physiologically exhausted, if the differentiated tissues undergo complete involution so that a new proliferation of germinal epithelium is required for the provision of gametes for the following breeding season, or if only a portion of the primordial germ cells develop each year, then the mode of differentiation of each season's crop can be determined by the impress of varying environmental circumstances, if these are of such a nature as to disturb sufficiently the general metabolism of the individual. Such would appear to be the explanation of Champy's results. Surgical removal of the gonad (*i.e.*, removal of the differentiated germinal epi-

thelium) will lead to the same result if following gonadectomy the general metabolism of the individual is influenced by special feeding (Harms, 1923).

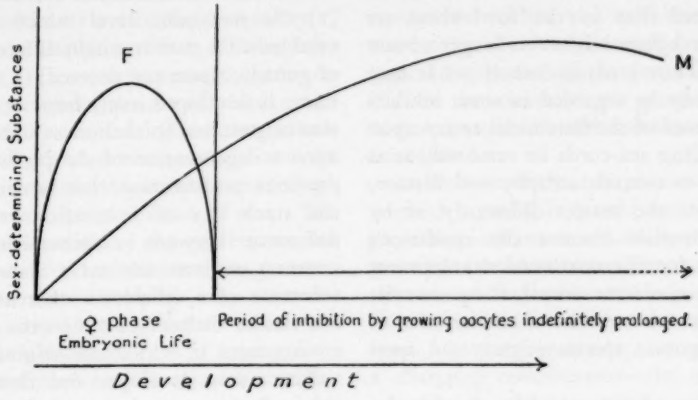

FIG. 1.

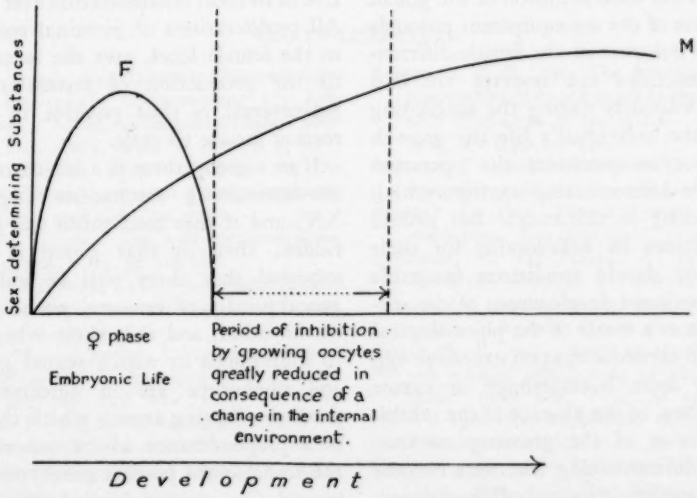

FIG. 2.

In the case of the fowl it has been shown that there are successive invasions of the organ by sex-cords derived from the peritoneum (Fell, 1923). The histological appearances suggest that so long as growing oocytes are present these invading sex-cords do not develop further into functional germinal tissue, perhaps being transformed into "luteal" cells. But in the absence of growing oocytes these cords are apparently converted regularly into seminiferous tubules. It would seem

that the physiological conditions which in the female embryo at the time of differentiation of the sex-organization induce the primitive germ-cells to assume the characters of oocytes—and it will be remembered that in the fowl these are laid down before birth—no longer obtain in the mature bird, so that if what may legitimately be regarded as some inhibiting influence of the functional ovary upon the invading sex-cords be removed, as is the case in ovarian atrophy and disease, or, to put the matter differently, if by certain ovarian diseases the conditions favorable for the continued development of the sex-cords are created, the germ-cells inevitably take on the characteristics of spermatogonia, spermatocytes, and spermatozoa.

If during embryonic life the female-determining substances are effectively in excess and the differentiation of the gonad and the rest of the sex-equipment proceeds under the influence of the female-differentiating reactions the oocytes are laid down. Ordinarily during the succeeding years of the individual's life the growth of the oocytes precludes the operation of the male-differentiating reactions which are increasing in efficiency. But should the conditions be unfavorable for their growth, or should conditions favorable for the continued development of the sex-cords arise as a result of the physiological exhaustion consequent upon excessive egg laying or from haemorrhage or tumor growth, then, in the absence of the inhibitory influence of the growing oocytes, the male-differentiating reactions become effective, spermatic tissue is differentiated, and the characters of the individual become as those of the male. It can be expected that almost any hen of a highly fecund strain will sooner or later develop some degree of the male characterization.

The fact that following ovariotomy of the hen there is developed in the right gonadic site a testis, is to be explained on the assumptions that (1) ovariotomy is followed by a significant modification of the basal metabolism of the individual; (2) the metabolic level which becomes established is that at which differentiation of gonadic tissue can proceed; (3) ovarian tissue is developed solely from a proliferation of germinal epithelium which follows upon a degeneration of the products of a previous proliferation that occurs about the sixth day of incubation, that the difference between differentiation into ovarian or into testicular tissues is a reflection of a difference inherent not in the tissues themselves but in the internal environment in which the original ambivalent tissue develops, and that at no other time save at about the sixth day of incubation are those conditions provocative of ovarian differentiation ever present. All proliferations of germinal epithelium in the female fowl, save the second, lead to the production of testicular tissue. Sex-reversal is thus possible in the direction female to male.

If in a group there is a sex-chromosome sex-determining mechanism (*e.g.*, XY: XX) and if this mechanism can be overridden, then in that group it can be expected that there will be individuals genotypically of one sex, phenotypically of the other, and that these when mated to individuals in which sexual genotype and phenotype are in agreement will produce offspring among which there will be a preponderance of the sex to which the transformed parents genotypically belonged (*i.e.*, a transformed female functioning as a male will yield a preponderance of females; a transformed male functioning as a female will yield a preponderance of males). If this process of transformation affects the individuals of several generations and thereafter ceases

to act, there will be a decreasing preponderance of one sex followed by a preponderance of the opposite sex in the first generation after the close of the period during which sex-transformation has occurred and finally a sex-ratio of equality.

It is to be emphasized that, although the processes of sex-differentiation are reversible, the genotypic sex of an individual is not thereby affected. The monogametic individual remains monogametic and the digametic remains digametic, even though it elaborates sperm instead of ova. The form and function of the gamete are not determined by its chromosome content, they are determined by the structure and function of the gonad in which the gamete is elaborated.

The profound modification of sexuality induced by alterations in metabolic level has persuaded some investigators to the conclusion that sex fundamentally is not an affair of the chromosomes and genes, but that it is the physiological properties of the zygotes that determine sex; but surely it is reasonable to hold that the conditions within the cell are nothing more than the sum total of the physiological expression of the genes in action. It is in the action of the genes that this or that type of initial metabolism becomes established.

In the case of those forms in which sex-reversal is usual it would seem that the physiological state established by the genotype is readily overridden through the impress of environmental agencies and that sex-reversal is common because this is so. Reversal is an adaptive response to a changing environment—the individual is a female when it may be and a male when it must.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will usually appear in each number one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

EVOLUTION

MODERNISM. *What It Is. What It Does. Whence It Came. Its Relation to Evolution.*
By J. M. Stanfield.
The Christian Alliance Publishing Co.
$1.50 $4\frac{3}{4}$ x $7\frac{1}{2}$; 217 *New York*

So far in our *Fundamentalist Portrait Gallery* we have only had depictions of persons who, in a sense, might be called derivative Fundamentalists. This time we are pleased to be able to present in Mr. J. M. Stanfield a representative of the real, basic, autochthonous stock, a *Tennessee* Fundamentalist.

In an introduction by Professor Leander S. Keyser of the Hamma Divinity School, it is stated that Mr. Stanfield "is a layman, not a professional theologian." This seems entirely credible, after reading the book. But Professor Keyser follows it with another statement that: "He cannot, therefore, be accused of having 'an axe to grind' or a special religious bias." Here, again after reading the book, we feel compelled to part company intellectually with Professor Keyser. To us Mr. Stanfield seems, throughout his treatise, to glory in his religious bias, and to whet his axe for the necks of modernists and evolutionists with a single-minded fervor which compels our admiration for its hundred-per-cent thoroughness. He gives no quarter and asks none. There is no slopping or staining of the pages with the milk of human kindness. Mr. Stanfield knows precisely what he thinks of modernists and evolutionists and he tells them and the world.

The book is divided into three parts. The first devotes itself to modernism as a theological doctrine, the second to evolution, and the third to the development of these heresies in the Protestant churches. The forthrightness of the theological position is sufficiently illustrated by the following quotation.

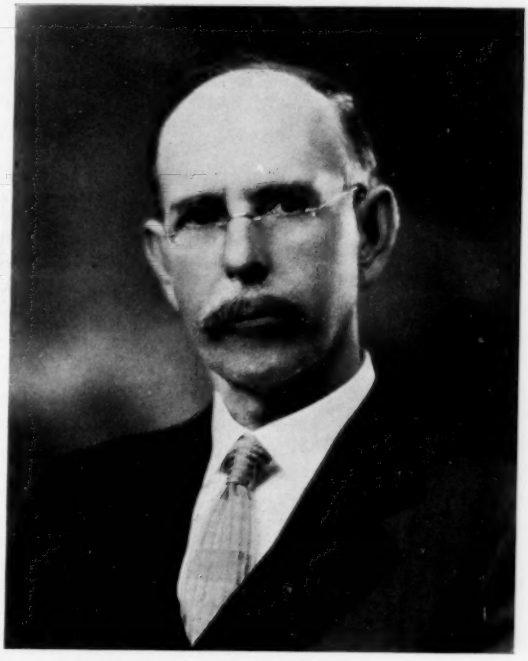
> Since God is all-wise and cannot lie, and is the Author of the whole Bible, according to the orthodox view; all statements in the Bible involving science or history must be true, notwithstanding the fact that the Bible was meant to teach religion. If the Bible was full of errors, as the Modernists claim, it could not reveal a God of truth nor teach righteousness. Error cannot reveal truth nor the God of truth.

Regarding evolution Mr. Stanfield has no patience with the "reconcilers." He prints a long quotation from a book by one Dr. Marion Shutter, which seems to us to be a singularly pious statement of evolution from the standpoint of a "rec-

onciler," and then proceeds to discuss it as follows:

This is Theistic Evolution. Notice some of the blasphemous heresies just this quotation includes; treats the Genesis account of the creation of man as untrue and affirms a brute origin for man; denies that man was first holy, but teaches that he emerged from the animal, a savage and without revelation from God, learned righteousness through his own efforts and experiences. At first he was without moral responsibility, knew no God, but after "uncalendared ages" achieved the idea of one.

You notice the Bible as a revelation is ignored, and this Theistic evolutionist calls the Genesis account a "baseless fabric of a vision"! Then he shows his belief that the Bible is untrue by teaching that there has never been a curse, nor sin and fall; men are not under condemnation, no devil, no wrath of God, no hell, no need for the atonement of Christ as a substitute for sinners. Christ was not God incarnate born of a virgin, but he blasphemously teaches that Christ also is a child of evolution, which means that he came from the brute, but because he had the good blood of Abraham, David and the prophets in him, he becomes a good example for us! And lastly, God, men and nature are all one in essence. Shutter rather obscures this thought but you can see that it is there. So the difference between Atheistic, or infidel, evolution and Theistic evolution is just about "six of one and a half dozen of the other;" both have the same origin, general principles and object.



J. M. Stanfield, of Cleveland, Tennessee

Farther on Mr. Stanfield says:

Evolution is the result of a desire to oppose and contradict the truths of divine revelation. This is plainly and frankly stated by Huxley in *Science and Hebrew Tradition*, as follows: "These essays are for the most part intended to contribute to the process of destroying the infallibility of Scripture." And yet with all this effort of these learned skeptics, not a single known or genuinely proven fact in any department of science, history or archaeology has been found to be in conflict with the real teaching of the Bible and the Christian religion. Lord Kelvin, the

great English scientist, states it thus: "There is not a single ascertained fact of science which conflicts with any statement of the Bible." The real scientists are not skeptics. We mention a few as Kepler, Newton, Davy, Linnie Lavoisier, Maedler (who said, "A real scientist cannot be an infidel"), Virchow and our own Howard A. Kelley.

Why "Linnie Lavoisier" we cannot guess, unless it be a misprint for "Linné, Lavoisier." But it is cheering to see our friend Dr. Kelley in such high-toned company.

From this book, on which we can waste no more space, biologists will get a clearer picture of the devastating implications of the Tennessee brand of Fundamentalism than from any other we have seen. If the ideas it embodies were to prevail the Dark Ages would seem, by comparison, to have been a veritable paradise of light and learning.

THE DENTITION OF DRYOPITHECUS AND THE ORIGIN OF MAN.
By William K. Gregory and Milo Hellman. *American Museum of Natural History* $1.50 *New York*
$6\frac{1}{2}$ x $9\frac{1}{2}$; 123 + 25 plates (paper)

The chief results of this beautifully illustrated, extremely thorough morphological contribution to our knowledge of the human family tree are:

To judge from the characters of the dentition the modern anthropoids, taken as a whole, are unquestionably man's nearest relatives among all known mammals; conversely, no other known living or fossil mammals can seriously contest this claim of the anthropoid group. We therefore prefer to accept this direct evidence and to trace the evolution of the human dentition through that of the primitive anthropoid *Dryopithecus* back to the primitive tarsioid *Parapithecus*, rather than to invent entirely hypothetical and unknown stages leading back to unknown stem forms of pre-primates in the Paleocene or Upper Cretaceous. Each existing anthropoid has specialized away from the common ancestor in certain respects. When all due allowance for these specializations has been made, the chimpanzee is far less specialized away from the common stem form than is man. The various extinct anthropoids known as *Dryopithecus* are decidedly nearer to the common stem form than are any of the modern giant anthropoids.

From some form of *Dryopithecus* possibly related to *D. rhenanus* man has inherited his dental formula, the "Bicuspid" pattern of the upper and lower premolars, the "*Dryopithecus* pattern" of the molars, many details of the incisors and canines and many important characters of the deciduous dentition. It may be noted that this is not a light speculation but is based on observations of the characters actually inherited in the more primitive human dentitions, apparently from a *Dryopithecus*-like ancestor.

PURPOSIVE EVOLUTION. *The Link Between Science and Religion.*
By Edmund Noble. *Henry Holt and Co.* $5.00 (Student's edition $4.00) *New York*
$5\frac{1}{4}$ x $8\frac{1}{2}$; xi + 578

A discussion of the hoary problem of teleology, by a person who can at least write well, whatever one may think of his philosophical powers. The thesis developed is that

purposiveness is a principle rooted in things, not a value at some point in time and place added to things—as the ways in which, through directed motion, ends are reached in both animate and inanimate, not as the consciousness of such ways. The vital activities of the organism, internal and relational, unconscious and conscious, are seen to derive from the self-maintaining activities of the universe; their purposive character is traced to a cosmos which is end-reaching before the coming of life and "intelligent" before the advent of consciousness. Natural selection, while retained as an eliminating factor, is relieved from the impossible task of giving rise to those variations which it only helps to conserve but cannot have any part in originating: by advance beyond the Darwinian theory to recognition of a purposive process in Nature we are enabled to pass from the "origin of species" to the origin of the organism, and from an obviously inevitable "survival of the fittest" to realization of why and how the fittest arrive.

This argument can, of course, arrive only at one terminus—God. It fails entirely to answer the impudent question

first raised by a paleolithic school boy in the Academy at Les Eyzies: "If God is responsible for the purposiveness observable in the order of nature, who, then, made God?"

THE NATURE OF THE WORLD AND OF MAN.

By Sixteen Members of the University of Chicago Faculty.

H. H. Newman, Editor.

The University of Chicago Press

$4.00 6 x 8¾, xxiv + 566 *Chicago*

The specifically biological chapters in this latest addition to the now so popular type of coöperative literature are the following: The Nature and Origin of Life, and The Factors of Organic Evolution, by H. H. Newman; The Bacteria, by E. O. Jordan; The Evolution of the Plant Kingdom, by M. C. Coulter; Interactions between Plants and Their Environment, by H. C. Cowles; The Evolution of the Invertebrates, by W. C. Allee; The Evolution of the Vertebrates, by Alfred S. Romer; The Coming of Man, by F.-C. Cole; Human Inheritance, by E. R. Downing; Man from the Point of View of His Development and Structure, by G. W. Bartelmez; The Dynamics of Living Processes, by A. J. Carlson; Mind in Evolution, by C. H. Judd. The book is the outcome of a general "survey" course. The quality of the different contributions naturally varies. But taken as a whole the book has real, if ephemeral, value.

SPIRITUAL EVOLUTION AND THE BIBLE.

By Edna F. Lee.

The Christopher Publishing House

$1.00 5 x 7½; 44 *Boston*

It is probable that the late Mr. Bryan would have held this sincere little tract in as low esteem as he did the writings of scientific men. It is a reconciliation document by a deeply religious person. Reconciliation is here achieved in the simplest of conceivable ways. All the results of science, past, present and future, whatever they may be, are cheerfully and naively accepted at their face value. They are held to represent the awkward and groping approach of mankind to a realization and understanding of what God's plan was and is. "We need not know the details of the theory of Evolution to believe in the general principle, for the world before us is saturated with proof of the struggle upward, and not only physically but spiritually." Mrs. Lee is obviously neither a great scholar nor a great philosopher. She probably does not in the smallest degree realize how similar her cosmic philosophy, arrived at by the simplest minded faith, is to that of some of the profoundest thinkers who have struggled with the problem. Her terminology is, to be sure, different from theirs. But that is unimportant.

GENETICS

ELEMENTE DER EXAKTEN ERBLICHKEITSLEHRE. *Mit Grundzügen der Biologischen Variations-statistik.*

By W. Johannsen. *Gustav Fischer*

Mk. 32 *Jena*

6¼ x 9¼; xi + 735 (paper)

The third edition of this classic of genetics appears thirteen years after the second, which has been out of print for more than seven. Naturally much revision has been required. Genetics has made great strides in the last decades. But the general plan of the "thirty lectures" remains much as before, which

means that the book is broader in the distribution of its emphasis than are some of the current American and English texts on genetics. Johannsen made a very great contribution to our knowledge of heredity. The interest of biologists in this field has swung in another direction and his work has in some sense been overshadowed. But its fundamental soundness and importance has not in the least been altered by this circumstance.

POTATO VARIETIES.
By Redcliffe N. Salaman.
The Macmillan Co.
$8.50 7 x 10¼; xxii + 378 *New York*

A thorough, sound, and penetrating contribution to plant genetics, by the foremost investigator of the field covered. For twenty years past Dr. Salaman has devoted himself to the study of the genetics of the potato. In this book he summarizes and critically evaluates, from the background of this rich experience, a great deal of what is known of the subject. The first twenty-three chapters deal with the general genetic problems which arise in connection with the cultivation of this important crop, while the remainder of the book deals with the description, history and synonomy of European varieties. There is a bibliography of 177 titles, and a detailed index. The book is illustrated with nine plates, beside text figures.

BREEDING AND IMPROVEMENT OF FARM ANIMALS.
By Victor A. Rice.
McGraw-Hill Book Co., Inc.
$3.50 5¾ x 9; xiv + 362 *New York*

A text book of animal breeding for use in agricultural colleges. It follows conventional lines in the treatment of the various topics covered, but good pedagogical judgment is shown in the arrangement of the material. Emphasis is rightly placed, considering the purpose of the book, on the practical aspects of the subject.

ÜBER DIE ZEICHNUNGEN DER BLÄTTER UND BLÜTEN.
By Ernst Küster.
Urban und Schwarzenberg
Rm. 7.20 *Berlin*
7 x 10; iv + 82 (paper)

A systematic discussion of variegation in leaves and blossoms, with numerous photographic illustrations. It will prove a useful reference work for plant geneticists. There is an index of genera only.

GENERAL BIOLOGY

LOCAL IMMUNIZATION. *Specific Dressings.*
By A. Besredka. Edited and translated by Harry Plotz. The Williams & Wilkins Co.
$3.50 5½ x 8¾; xi + 181 *Baltimore*

This is an important book, containing a great deal of original and interesting material, but it is written with so little sense of literary form that it leaves an impression of general vagueness and lack of precise thinking. This is most unfortunate because the author's experimental work and the theoretical conclusions to which it has led, are in the highest degree important. They amount really to a complete alteration of currently accepted views regarding the biology of immunity. Besredka believes that immunization is essentially a local phenomenon. Thus in the case of such diseases as dysentery,

typhoid fever, paratyphoid or cholera, he pictures the phenomenon in this way:

> There exist in the various organs of higher animals, highly differentiated cells which act as local phagocytes. These cells enter into reaction only with certain definite viruses, contrary to the action of the leucocytes or motile phagocytes. The latter attack indiscriminately all foreign bodies; whether they be living or dead.
>
> It is these receptive cells, which are the exclusive property of highly differentiated beings, that have a specific affinity for certain viruses. It is fixed phagocytes—cells of the reticulo-endothelial layer, intestinal lymphatic cells or other cells—that direct the chemotactic movement of the free phagocytes and assure, with the aid of the latter, the immunity of the entire animal organism.

The book will well repay reading.

SYMBIONTICISM AND THE ORIGIN OF SPECIES.
By Ivan E. Wallin.
The Williams & Wilkins Co.
$3.00 6¼ x 9¼; xl + 171 *Baltimore*

"Symbionticism" is a term coined by Wallin to indicate the "universal presence of microörganisms within the cells of all plants and animals." It is the end result of "prototaxis," which is defined as "the innate tendency of one organism or cell to react in a definite manner to another organism or cell." This theory of symbionticism is based on the assumption that mitochondria are bacterial in nature. The author set out in 1919 to prove this and evidently convinced himself that mitochondria are really bacteria. On this assumption he proceeds to explain practically all of the fundamental problems of biology, including the phenomena of heredity and organic evolution. So far as known to the reviewer no first-rate investigator agrees with him. The book contains a considerable amount of interesting material on mitochondria and symbiosis.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 213.* Containing following articles: *Histologische Methoden und Ergebnisse der Mikroskopie im auffallenden Licht*, by Paul Vonwiller; *Die Nuclealfärbung*, by Robert Feulgen; *Verfahren, um den isolierten Hundekopf durch Anastomose mit dem Blutkreislauf eines anderen Hundes überlebend zu halten*, and *Perfusion des "isolierten" Kopfes vom "isolierten" Herz-Lungen-Präparat aus beim selben Hund*, and *Verfahren zur Hyper- und Hypothermisation der Säugetiere durch Erwärmung und Abkühlung des Blutes des durch Anastomose verbundenen carotidojugulären Kreislaufes*, and *Versuchsanordnung zur fraktionierten und kontinuierlichen quantitativen Bestimmung des CO_2 der Exspirationsluft*, by J. F. Heymans and C. Heymans; *Die Verwendung isolierter, lebender Membranen zum Studium der Permeabilität*, by Ernst Wertheimer; *Das Prinzip des absoluten Optimums in der vergleichenden Physiologie*, by Väinö Krohn.
Urban und Schwarzenberg
Mk. 7.80 7 x 10; 156 (paper) *Berlin*

This number of the Abderhalden handbook deals with a wide range of subjects, not closely related to each other. The last essay in the volume is an important one, which should be read by every experimentalist. It is a first rate contribution to scientific methodology.

ESSAYS IN POPULAR SCIENCE.
By Julian Huxley. *Alfred A. Knopf, Inc.*
$4.00 *New York*
5½ x 8½; xvi + 316

These essays, which cover a wide range of subjects, make pleasant and easy reading, and would seem likely to captivate such an audience as that of the Atlantic Monthly, for example. The professional biologist will be here and there shocked

at the easy and graceful sureness about matters which he had supposed were not only debatable but actively under debate. This attitude seems to be regarded as essential to successful popular scientific writing, and we accept it as we do many other current manifestations of the *mores*, which we cannot quite rationalize. But it *is* difficult to be properly serious when we are told that why more boy babies die is because boys have more semi-lethal genes in their chromosomes than do girls!

A BIBLIOGRAPHY OF AMERICAN NATURAL HISTORY. *The Pioneer Century, 1769–1865. The Rôle Played by the Scientific Societies; Scientific Journals; Natural History Museums and Botanic Gardens; State Geological and Natural History Surveys; Federal Exploring Expeditions in the Rise and Progress of American Botany, Geology, Mineralogy, Paleontology and Zoology.*

Vol. I. An Annotated Bibliography of the Publications Relating to the History, Biography and Bibliography of American Natural History and its Institutions, during Colonial Times and the Pioneer Century, which have been published up to 1924; with a Classified Subject and Geographic Index; and a Bibliography of Biographies.

Vol. II. The Institutions which have contributed to the Rise and Progress of American Natural History, which were Founded or Organized between 1769 and 1844.

By Max Meisel.

The Premier Publishing Co. *Brooklyn, N. Y.*

Vol. I, $5.00 $5\frac{3}{4}$ x 9; 244
Vol. II, $7.50 $5\frac{3}{4}$ x 9; xii + 741

This is a monumental piece of exact and painstaking bibliographical research, which will be an invaluable resource to the student of the history of science in America. A third volume is yet to appear. In the second volume the detailed citation of papers relating to natural history is preceded by a brief but extraordinarily useful history of the society or institution which published them. American biologists cannot do less to express their appreciation of the colossal labors of Mr. Meisel in their behalf than to see to it that a complete set of this Bibliography is on the shelves of their libraries.

THE MEMORY FACTOR IN BIOLOGY. *A Sketch of the Unity of Life.*

By C. J. Patten. Baillière, Tindall and Cox *London*
5 shillings 4 x $6\frac{1}{2}$; xiii + 175

This book, like its author's "Passing of the Phantoms," reviewed in these pages last year, contains a lot of matter about the habits and behavior of animals, particularly birds, which is interesting, if not always very critical. The general thesis of the book is to support the views of Hering, Samuel Butler, Semon, and Rignano, regarding the biological importance of memory.

LE BACTÉRIOPHAGE ET SON COMPORTEMENT. *Deuxième Édition.*

By F. d'Hérelle. *Masson et Cie.* *Paris*
$1.72 $6\frac{1}{2}$ x 10; 551 (paper)

A revised second edition of d'Hérelle's well-known treatise. A notice of the English translation has already appeared in THE QUARTERLY REVIEW OF BIOLOGY. It is a book which no student of general biology should fail to read, whether he is otherwise interested in immunology or not.

DER NEO-DARWINISMUS *metaphysisch begründet durch das Allgemeine Zweckmässigkeitsgesetz.*

By Victor Schiffner. *Gustav Fischer* *Jena*
Mk.2 $6\frac{1}{4}$ x $9\frac{1}{4}$; 50 (paper)

A philosophical discussion of adaptation. The author's "Neo-Darwinism" has a somewhat different connotation than that implied in the usual use of the word. He proposes to use this term to cover all "laws" which have to do with changes of living things, and under its aegis to synthesize all these into one "*Allgemeine Zweckmässigkeits-Gesetz.*"

THE MEANING OF DISEASE. *An Inquiry in the Field of Medical Philosophy.*
By William A. White.
The Williams & Wilkins Co.
$3.00 5 x 7½; 220 *Baltimore*

An interesting, well-written philosophical speculation regarding the biology of health and disease. Biologists will probably furnish a more sympathetic audience for the book than will most physicians, who as a group are, at the moment, thinking in different channels than Dr. White.

FATALISM OR FREEDOM. *A Biologist's Answer.*
By C. Judson Herrick.
W. W. Norton and Co., Inc.
$1.00 4¼ x 6½; 96 *New York*

The conclusion reached is that "A denial of the reality and efficacy of my power to shape my own character in accordance with consciously fabricated ideals and so to exercise genuine freedom to enlarge, purify, and ennoble my personality is a reversion to a primitive and tawdry fatalistic mythology of a barbarous age."

Sub specie aeternitatis Benedictus de Spinoza damnatus est.

BRIEF BIOLOGY.
By Charles Gramet (revised in collaboration with John F. Hummer). *Globe Book Co.*
67 cents *New York*
5 x 7¼; v + 218 (paper)

This text book of biology is "brief" in the sense that the economy of diction appropriate to telegraphic communication is used to convey to students of high-school grade a working knowledge of the plant and animal kingdoms in their entirety, including anatomy, physiology, psychology, anthropology, medicine, public health, etc. Perhaps this is sound pedagogy, but it wears a ghastly mien.

DE LA DURÉE DES ÊTRES VIVANTS. *Facteurs qui relèvent ou abaissent l'énergie vitale, qui prolongent ou raccourcissent la vie.*
By Éd. Retterer. *Gaston Doin et Cie.*
10 francs 5½ x 9; 188 (paper) *Paris*

A review of the literature on the biology of senescence and death, with particular emphasis on the rôle of the endocrine organs in these matters, and with a more sympathetic attitude towards the potentialities of surgical procedures as a means of rejuvenation than many biologists are disposed at present to assume.

GENERAL AND PROFESSIONAL BIOLOGY *with Special Reference to Man. Vol. I, General Biology. Vol. II. Introductory Embryology (Chick, Frog, and Mammal) and Comparative Anatomy.*
By Edward J. Menge.
The Bruce Publishing Co.
Vol. I, $3.50 6 x 9; 484 *Milwaukee*
Vol. II, $4.00 6 x 9; 498

The second edition of a text book of biology which, in a number of particulars, follows novel lines. The range

covered is enormous, the treatment of each subject is telegraphic in its brevity, and the rhythm of the composition is syncopated. It is a curious book.

HÄMATOLOGISCHES PRAKTIKUM.
Für Studierende und Ärzte.
By Hans Ziemann. *S. Karger*
M. 7.20 5½ x 8½; viii + 166 *Berlin*

A comprehensive, though brief, practical handbook on the general biology and pathology of the blood, with technical directions for the study of these subjects.

HUMAN BIOLOGY

RITUAL AND BELIEF IN MOROCCO.
Volumes I and II.
By Edward Westermarck.
The Macmillan Co.
$15 for set *New York*
5½ x 8½; Vol. I, xxxii + 608
Vol. II, xvii + 629

The author of *The History of Human Marriage* makes a contribution in the present volumes destined to rank as of perhaps even greater significance than his former work, which has long been a reference classic in the field of human biology. Professor Westermarck went to Morocco in 1898, as the first stop on a contemplated journey to various countries "to acquire first-hand knowledge of some forms of culture which differ from our own." He never went any farther. In the period between 1898 and 1926 he has made 21 journeys to Morocco, and spent there altogether seven years. The knowledge gained in this long, repeated, and intimate association with the Moroccans is embodied in this book. It is a contribution of the very first rank to anthropology, ethnology, psychology, and sociology. In addition to the author's wide and penetrating observations at first-hand, he has an encyclopedic knowledge of the literature, and every point is correlated and integrated with prior knowledge, with precise documentation. There is a really satisfactory index, covering 69 pages close set in eight point type. Altogether this is a monumental work, as interesting as it is sound. Our more wicked readers will find Chapter IX, "Curses and Oaths," not only entertaining but perhaps, on occasion, useful. We have something to learn from the Moroccans in this branch of polite accomplishments.

THE HISTORY OF WITCHCRAFT AND DEMONOLOGY.
By Montague Summers.
Alfred A. Knopf, Inc.
$5.00 6 x 9; xv + 353 *New York*

How this curious treatise came to get incorporated into the *History of Civilization* series is difficult to understand. For it is a theological tract in defense of witchcraft, *by one who believes in witches!* In making this statement our only defense against the charge of spoofing is the book itself. Read it!

And this is not all:

> Modern Spiritism is merely Witchcraft revived. The Second Plenary Council of Baltimore (1866), whilst making ample allowance for prestidigitation and trickery of every kind, warns the faithful against lending any support whatsoever to Spiritism and forbids them to attend seances even out of idle curiosity, for some, at least, of the manifestations must necessarily be ascribed to Satanic intervention since in no other manner can they be understood or explained.

The book is enormously erudite. The annotation and documentation is colossal, the bibliography extending to over 30 pages of fine print. The answer to the

old query "Can you beat it?" is clear. You can't!

GENIUS. *Some Revaluations.*
By Arthur C. Jacobson. *Greenberg*
$2.50 5¼ x 8¼; 160 *New York*

This is an entertaining book, which will be instantly condemned to the Index as blasphemous and heretical by every orthodox eugenical pontiff. For its thesis is that: "It is in the outcast, disinherited, vagabond, criminal, defective, insane and generally abnormal elements of humankind that genius germinates, never in the well-bred, eugenically speaking, Right Wing of the race. Let the 'respectable' wince if galled by this challenging truth."

The word "never" seems to us unfortunate in the first sentence quoted. But an author who has assembled such an interesting lot of evidence as Dr. Jacobson has, may perhaps be permitted a little exuberance. It is unfortunate that his book will not be much read by eugenists.

NATIVE DIET. *With Numerous Practical Recipes.*
By Ettie A. Rout. *William Heinemann*
6 shillings 5¼ x 8½; ix + 140 *London*

Like everything that Ettie Rout writes this book is interesting. It is propaganda for modified vegetarianism. The only meat food recommended is the flesh of fish or birds. About half the book is devoted to a discussion of the food habits of the Maori before contact with civilization, and the other half with recipes. The book ought not to be allowed to circulate in the United States because it contains the following sentences, which can only be regarded as an insult to the Constitution: "Our personal health would greatly improve if we took light herbal beers (home-made) instead of the large quantities of strong tea and coffee many of us drink. Home-brewed ale is a natural aperient. . . . . Ales and beers are very little trouble to make—there are plenty of recipes available—and when made at home they are extraordinarily cheap."

PRINCIPLES OF HUMAN GEOGRAPHY.
By P. Vidal de la Blache. Edited by Emmanuel de Martonne. Translated from the French by Millicent T. Bingham.
Henry Holt and Co.
$5.00 (Student's *New York*
edition $4.00) 5½ x 8½; xv + 511

Vidal de la Blache was the founder of the modern French school of geography, which in some important respects leads the world in this field. The present work is posthumous. The manuscript was in a highly unfinished state at his death, and while the completion by other hands has been skilfully done, it is obviously not the book that it would have been if its author could have finished it. It is a distinct service to have made so excellent an English translation as this is. A good deal of the author's salty style has been preserved. Students of the population problem, and of human biology generally, will want to read it.

ORIGINS OF EDUCATION AMONG PRIMITIVE PEOPLES. *A Comparative Study in Racial Development.*
By W. D. Hambly. *The Macmillan Co.*
$7.50 5¾ x 8¾; xx + 432 *New York*

The education of primitive children proceeds along lines similar to the education of wild animals. Through play activities, with a certain amount of parental correction and guidance, the

young savage learns how to avoid at least the major dangers which lurk in the biological and physical environment, and how to turn cosmic forces and situations in some degree to his advantage. It is a useful thing to have the scattered information on the education of primitive children collected, and critically organized and evaluated as it is in this interesting and sound treatise. The book is copiously illustrated with excellent photographs, and has an extensive bibliography and index.

DAS PROBLEM DER MENSCHWERDUNG.

By L. Bolk. *Gustav Fischer*

2.10 marks 6½ x 9½; 44 (paper) *Jena*

In this lecture before the 1926 meeting of the German Anatomical Society, the distinguished author points out that the problem of human evolution has two sharply separated aspects. One is the phylogenetic relationship of man to the other primates. The other is the genesis of the human form. It is the second of these problems with which he is concerned. He develops the thesis that the human form is the resultant of a progressive evolutionary "fetalization," the causal factors for which are to be found in the endocrine system.

THE SIGNIFICANCE OF THE PHYSICAL CONSTITUTION IN MENTAL DISEASE.

By F. I. Wertheimer and Florence E. Hesketh.

The Williams & Wilkins Co.

$2.50 *Baltimore*

6 x 9; xiii + 76 + 5 plates

This study of the relation of physical constitution to mental disease is based upon the careful anthropometric measurement of a long series of bodily dimensions in nineteen cases of affective (manic-depressive) psychopathic personalities and psychoneuroses; and ten cases of organic reaction type including epilepsy. A new index is described, which is said to differentiate "exactly" the clear asthenic, athletic, and pyknic types of Kretschmer. There is a bibliography of 95 titles, but no index.

INFANT MORTALITY AND ITS CAUSES. *With an Appendix on the Trend of Maternal Mortality Rates in the United States.*

By Robert M. Woodbury.

The Williams & Wilkins Co.

$3.50 5⅜ x 8; x + 204 *Baltimore*

This book is mainly a reprint of separate papers on various aspects of infant mortality, originally published while the author was statistician of the Childrens' Bureau of the Department of Labor in Washington. It contains a considerable amount of material of interest to the student of human biology, though it makes no considerable addition to already existing knowledge. There is a detailed index.

AN INTRODUCTION TO THE HISTORY OF MEDICINE. *From the time of the Pharaohs to the end of the XVIIIth Century. By Charles G. Cumston. With an Essay on the relation of History and Philosophy to Medicine by F. G. Crookshank.*

Alfred A. Knopf, Inc.

$5.00 6 x 9; xxxii + 390 *New York*

A history of medicine intended primarily for the general reader, and secondarily as an introduction to the subject for the student of medicine. Both these purposes it serves extremely well. It is

one of the happiest additions which the English editor of *The History of Civilization* series (Mr. C. K. Ogden), has made to the French series *L'Évolution de l'Humanité*.

UNFRUCHTBARKEIT ALS FOLGE UNNATÜRLICHER LEBENSWEISE. *Ein Versuch, die ungewollte Kinderlosigkeit des Menschen auf Grund von Tierversuchen und anatomischen Untersuchungen auf die Folgen des Kulturlebens zurückzuführen.*

By H. Stieve. *J. F. Bergmann*

RM. 3.60 6¾ x 10; 52 (paper) *Munich*

Describes a series of experimental investigations showing the deleterious effects of bad environmental conditions, poisons, inadequate food, bad housing, etc. upon the gonads of rats, poultry, etc. From these results the conclusion is reached that the "unnatural" environmental conditions of modern civilization are a major factor in the decline of the human birth-rate. The evidence does not quite prove the conclusion.

VERHANDLUNGEN DER GESELLSCHAFT FÜR PHYSISCHE ANTHROPOLOGIE. *Vorträge gehalten am 13. und 14. April 1926 auf der ersten Tagung in Freiburg i. B. Band I.*

Herausgegeben vom Vorstand der Gesellschaft. Anthropologischen Institut der Universität München

Mk. 6 *München*

6½ x 10; 78 + 10 plates (paper)

This report of the first meeting of the German Society for Physical Anthropology contains ten interesting papers by members. It is a pleasure to call the attention of American workers to this new society and its publication. These facts testify to the growing recognition of physical anthropology as a special and separate discipline. The *Verhandlungen* are published as a supplement to Volume III of the *Anthropologischer Anzeiger*.

THIS BELIEVING WORLD. *A Simple Account of the Great Religions of Mankind. By Lewis Browne.* *The Macmillan Co.*

$3.50 5½ x 8½; 347 *New York*

This "best seller" is an entertaining contribution to human biology. It tells the story of the manner in which the world's great religions developed, with especial emphasis on the basic motivating element, fear of Nature and its phenomena. We recommend the book strongly to the young. We have seen no better prophylaxis against Fundamentalism.

HYGIEIA *or Disease and Evolution.*

By Burton P. Thom. *E. P. Dutton and Co.*

$1.00 4¼ x 6; 107 *New York*

This number of the Today and Tomorrow series discusses the evolution of disease and its influence upon the past and future evolution of man. The general conclusion reached is that a "gloriously golden" future impends, "when misery will be no more, and peace, and health, and happiness will reign supreme." We hope the author is right about this.

KIND UND VOLK. *Der Biologische Wert der Treue zu den Lebensgesetzen beim Aufbau der Familie. Erster Teil, Vererbung und Auslese. Zweiter Teil, Gestaltung der Lebenslage.*

By Hermann Muckermann.

Herder und Co. Freiburg

Teil 1, Mk. 3.60 5 x 7¼; xii + 253

Teil 2, Mk. 3.80 5 x 7¼; 290

The "11th to 15th" edition of a treatise

for the general reader which deals with eugenics in the first volume, and a queer mixture of patriotism, babies, housing conditions and religion in the second. It seems unlikely to be of particular interest to American readers, but since over 28,000 copies have been sold there must be something about it which the Germans like.

CONSIDERATIONS REGARDING THE POSSIBLE RELATIONSHIP OF CANCER TO RACE BASED ON A STUDY OF ANTHROPOLOGICAL AND MEDICAL STATISTICS OF CERTAIN EUROPEAN COUNTRIES.

By Alfredo Niceforo and Eugène Pittard.

Health Organization, League of Nations

$3.00 $8\frac{1}{4}$ x $10\frac{1}{4}$; 330 *Geneva*

A most interesting study of the incidence of cancer, by a distinguished statistician and a distinguished anthropologist, working in collaboration. They are extremely cautious about drawing general conclusions, but the evidence they present certainly makes it probable that "the Mediterranean 'race' (*Homo mediterraneus*) is less subject to cancer than the Alpine 'race' (*Homo alpinus*) or the blond dolichocephalous 'race' (*Homo nordicus or europaeus*)."

DE LAMAR LECTURES 1925–1926. *The Johns Hopkins University, School of Hygiene and Public Health.*

Edited by W. H. Howell.

The Williams and Wilkins Co.

$5.00 6 x 9; 220 *Baltimore*

The papers in this collection of lectures on problems of hygiene and public health likely to be of greatest interest to the biologist are those of Smillie on "Intensity surveys of hookworm infestation," Goldberger on the "Etiology of pellagra," Dublin on "Body build and longevity," and Stockard on "Constitutional types in relation to disease."

CALIFORNIA ANTHROPOMETRY.

By Edward Winslow Gifford.

University of California Press

$2.25 *Berkeley*

$7\frac{1}{4}$ x $10\frac{3}{4}$; 173 + 52 plates

This volume presents an extensive series of measurements of California Indians and the constants, chiefly means, calculated from them. These data have been collected at various times during the past twenty years by members of the Department of Anthropology of the University of California. The plates present a great number of photographs of Indian types.

THE ARAB CIVILIZATION.

By Joseph Hell (Translated from the German by S. Khuda Bukhsh).

W. Heffer and Sons, Ltd.

8s.6d. *Cambridge*

$5\frac{1}{2}$ x $8\frac{1}{2}$; xvii + 128

Professor Hell's *Die Kultur der Araber* is an interesting account of the history of Mohammedanism, and its social consequences. This translation is well done, and derives added interest from the fact that the translator debates a number of points with his author.

THE EVOLUTION OF VALUES. *Studies in Sociology with Special Applications to Teaching.*

By C. Bouglé. Translated by Helen S. Sellars.

Henry Holt and Co.

$2.00 *New York*

$4\frac{3}{4}$ x $7\frac{3}{8}$; xxxvii + 277

An interesting, well documented and indexed discussion of human society from

the point of view of the significance of moral and various other sorts of values upon social behavior. There is an excellent introduction by Professor Roy Wood Sellars.

ERBLICHKEITSFORSCHUNG UND WIEDERGEBURT VON FAMILIE UND VOLK.
By Hermann Muckermann. *Herder und Co.*
Mk. 1.20 5 x 7⅛; 66 *Freiburg*

The fourth edition of a little treatise on eugenics, for popular consumption. It follows entirely conventional lines. All the standard horrible examples are present and voting.

FARM POPULATION OF THE UNITED STATES. *An Analysis of the 1920 Farm Population Figures, Especially in Comparison with Urban Data, Together with a Study of the Main Economic Factors Affecting the Farm Population. Department of Commerce, Bureau of the Census Monographs VI.*
By Leon E. Truesdell.
Government Printing Office
$1.75 *Washington, D. C.*
7 x 10; xi + 536

Of interest as a source book to students of human biology generally, and to students of the population problem in particular.

FRÜHSCHEIN DER KULTUR. *Bilder aus Vorgeschichte und Urzeit.*
By Johannes Ledroit. *Herder und Co.*
4.80 marks *Freiburg im Breisgau*
5¼ x 7¾; ix + 257

A brief popular account of man's development from paleolithic to iron age cultures. Not so good a book as several others in the same field.

AUF DER SPUR DES URMENSCHEN.
By Robert Lais. *Herder und Co.*
Mk. 3.50 *Freiburg*
5¼ x 8; viii + 183 (paper)

Just another brief popular "prehistory," with no particular merit to recommend it above others in its class.

ZOOLOGY

LA VIE DES TERMITES.
By Maurice Maeterlinck. *Eugène Fasquelle*
12 francs 4¾ x 7½; 217 (paper) *Paris*

A companion volume to *La Vie des Abeilles*. At the start Maeterlinck says that, being less young than when he wrote that book, it is even easier now than it was then to resist the temptation to depart from the exact scientific record in telling the story of the biology of termites. It is a charming book. But it is a little amusing to denizens of the Johns Hopkins University to be repeatedly told that L. R. Cleveland was enabled to carry out his important investigations on termites because of the wonderful resources of his laboratory at *Harvard* University!

BRITISH BIRDS. (*Volume IV*).
By Archibald Thorburn.
Longmans, Green and Co.
$5.50 6 x 9; x + 154 *New York*

This completes the popular priced edition of Thorburn's classic, previous volumes of which have been noticed in The Quarterly Review of Biology as they appeared. The orders represented in this volume are the Limicolae, Gaviae, Alcae, Pygopodes, and Tubinares. The plates are, of course, the great feature. The one for the woodcock in this volume is superb. But all are so good that it is really unfair

to pick out any particular one for special mention.

LES PIGMENTS DANS L'ORGANISME ANIMAL.

By J. Verne. *Gaston Doin et Cie.*
28 francs *Paris*
$4\frac{1}{2}$ x 7; xv + 603 (paper)

A thorough review of the present state of knowledge of animal pigments and their biological significance. There is a bibliography covering 43 pages, and a detailed index. The volume forms one number of the *Bibliothèque de Biologie Générale* edited by Professor Caullery, in the *Encyclopédie Scientifique*, of which other volumes have been noticed in these pages.

LES POISSONS ET LE MONDE VIVANT DES EAUX. *Études Ichthyologiques. Tome Premier. Les Formes et les Attitudes.*

By Louis Roule. *Librairie Delagrave*
30 francs $6\frac{1}{2}$ x 10; 359 (paper) *Paris*

Dr. Roule plans a monumental treatise on the natural history and biology of fishes, in nine volumes, of which this is the first. In it are discussed the general forms which fish take, long or short, fat or flat, flying or walking, etc. The book is well written, and illustrated with text figures and some 16 colored plates. It maintains a high standard of popular natural history writing.

THE INDIAN ZOOLOGICAL MEMOIRS ON INDIAN ANIMAL TYPES. I. PHERETIMA (*The Common Indian Earthworm*).

By Karm N. Bahl. *K. N. Bahl*
Rupee 1, annas 8 *Lucknow, India*
6 x $9\frac{1}{2}$; iv + 72

This is the first number in a proposed series of manuals of zoological types used in teaching in India. It gives a well-arranged, abundantly illustrated, and for class work quite sufficiently detailed account of the structural and functional anatomy of the earthworm.

MORPHOLOGIE DER TIERE IN BILDERN. *2. Heft. Protozoen; 2. Teil: Rhizopoden.*

By Alfred Kühn. *Gebrüder Borntraeger*
M. 18 *Berlin*
7 x $10\frac{1}{2}$; iv + 165 (paper)

This sample part suggests that the work as a whole will be a gorgeous zoological picture book, if other groups are treated in the same degree of detail that the rhizopods are. This number includes some 200 excellent drawings, with brief text, illustrating some 13 orders of rhizopods.

HADDOCK BIOLOGY. *III. Metabolism of Haddock and Other Gadoid Fish in the Aquarium. Fishery Board for Scotland Scientific Investigations. No. II.*

By Harold Thompson.
H. M. Stationery Office
2s. 6d. *Edinburgh*
$7\frac{1}{4}$ x $10\frac{3}{4}$; 14 + 4 plates (paper)

An interesting experimental study of the growth of the haddock, whiting, and codling in an aquarium, with a regulated and abundant food supply. The time rate of growth is increased by about 100 per cent over controls in the sea.

PLANKTON OF THE OFFSHORE WATERS OF THE GULF OF MAINE. *Bureau of Fisheries Document No. 968.*

By Henry B. Bigelow.
Government Printing Office
$1.25 *Washington, D. C.*
$7\frac{1}{2}$ x 11; 509 (paper)

This is the second part of the report on the oceanographic and biologic survey of

the Gulf of Maine. The first volume was noticed earlier in THE QUARTERLY REVIEW OF BIOLOGY. It is a monumental contribution to the subject of marine planktology.

COLLEGE ZOOLOGY.
By Robert W. Hegner. *The Macmillan Co.*
$3.50 5⅝ x 8½; xxiii + 645 *New York*

In this revised edition of a standard, widely-used text the author has made considerable alterations in the arrangement of the material, and has added some seventy new illustrations.

TIERPFROPFUNG. *Die Transplantation der Körperabschnitte, Organe und Keime.* (*Die Wissenschaft. Bd. 75.*)
By Hans Przibram.
Friedr. Vieweg und Sohn
17.50 Rm. *Braunschweig*
5½ x 8½; viii + 303 (paper)

A thorough and comprehensive review of the zoological literature on grafting and transplantation, which will be useful as a reference work. There is an extensive bibliography, covering thirty-six pages, and a detailed index.

PRACTICAL ANATOMY OF THE RABBIT. *An Elementary Laboratory Textbook in Mammalian Anatomy.*
By B. A. Bensley. *P. Blakiston's Son and Co.*
$3.00 5½ x 8⅛, 298 *Philadelphia*

The fourth edition of a well known and thoroughly established laboratory manual.

BOTANY

PHOTOSYNTHESIS.
By H. A. Spoehr. *Chemical Catalog Co.*
$6.50 6 x 9; 393 *New York*

This is a thorough critical review of the present state of knowledge regarding photosynthesis. The material is discussed under the following heads: The origin of organic matter and the cosmical function of green plants; the nature of photosynthesis as determined by observations of gaseous interchange and the formation of organic matter; the products of photosynthesis; the methods of measuring photosynthesis; the chemistry of photosynthesis; energy relations; chlorophyll and the chloroplast. The book is extensively documented, but all references are given in extremely abbreviated form as foot notes. We believe that the usefulness of this excellent and much needed reference treatise would have been enhanced if all the references to the literature had been collected in a bibliography with complete citation of titles. There are detailed author and subject indices.

AIMS AND METHODS IN THE STUDY OF VEGETATION.
Published by The British Empire Vegetation Committee. Edited by A. G. Tansley and T. F. Chipp.
The Crown Agents for the Colonies
12s. 6d. 5½ x 8¾; xvi + 383 *London*

A useful handbook of methods used in plant ecology, designed to give actual and potential workers a statement of what is meant by the ecological study of vegetation, and of the reasons why it is important scientifically and of great practical value. Part I deals with methods in general, and with the broad environmental factors. Part II contains five essays on different regions, tropical, subtropical, arid, etc. Part III discusses types of vegetation. In Parts II and III the chapters are contributed by different special experts on the subjects covered. The book is well illustrated and indexed.

LES FOUETS ET LE MOUVEMENT DES BACTÉRIES.

By Émile Frache. *Berger-Levrault*

$1.00 *Nancy*

6½ x 10; ix + 193 (paper)

The author of this extensive discussion of the morphology and physiology of bacteria strongly objects to the common usage which names the motor organs of bacteria "cilia" or "flagella." He wants these organs called "whips." The terminology seems relatively unimportant. What Dr. Frache has done is to make a thorough review of the literature, repeating many of the observations regarding the movements of bacteria and the organs by which they are produced. He seems to have contributed little that is new on his own account. There is a bibliography covering 16 pages, and four plates containing figures copied from the works of other bacteriologists.

OUTLINES OF THE HISTORY OF BOTANY.

By R. J. Harvey-Gibson.

The Macmillan Co.

$4.25 5¼ x 8½; x + 274 *New York*

An excellent general introduction to the history of botany, given originally as lectures to third-year students, by the professor in the University of Liverpool. It seems a pity that it is not illustrated, as the opportunity of useful and entertaining illustrations is so great in a general history of a branch of science, like this. There is a bibliography of 50 selected titles, intended merely as a guide to further reading in the field.

FOREST, STEPPE AND TUNDRA. *Studies in Animal Environment.*

By Maud D. Haviland (Mrs. H. H. Brindley) *The Macmillan Co.*

$5.00 5½ x 8¾; 218 *New York*

A chatty treatise on ecology, based primarily upon the author's visits to the desert tundras of Siberia in 1914, to the Steppes bordering the Danube in 1917, and to the forests of British Guiana in 1922. There is much material of general biological interest in the book. Two plates in black and white half tone to illustrate protective *coloration* are not very convincing.

THE CHEMISTRY OF CELLULOSE AND WOOD.

By A. W. Schorger.

McGraw-Hill Book Co., Inc.

$6.00 5½ x 8; xiv + 596 *New York*

While primarily a chemical treatise, the value of this book as a reference work to the botanist is enhanced by the fact that the author has kept in mind throughout that wood is a substance of biological origin. The literature is thoroughly reviewed, and there are detailed indices.

DIE ÖKOLOGISCHE MORPHOLOGIE DER PFLANZEN *im Lichte neuerer physiologischer und pflanzengeographischer Forschungen.*

By Hans Fitting. *Gustav Fischer*

1.80 marks *Jena*

6¾ x 10; 35 (paper)

A critical review, documented with a bibliography of 68 references, of the present state of knowledge regarding the morphological effects of environmental forces upon plants, presented by the distinguished professor of botany at Bonn, as an address before the 1926 meeting of the German Botanical Society.

THE FERNS (FILICALES). *Treated Comparatively with a View to Their Natural Classification. Volume II. The Euspo-*

rangiatae and Other Relatively Primitive Ferns.
By F. O. Bower. *The Macmillan Co.*
$10.00 7 x 10¼; 344 *New York*

A morphological treatise dealing with fifteen families of ferns, chiefly from the phylogenetic viewpoint, with abundance of illustration and bibliographic documentation. It sustains the author's high reputation for painstaking thoroughness.

AN INTRODUCTION TO PLANT ANATOMY.
By Arthur J. Eames and Laurence H. MacDaniels. *McGraw-Hill Book Co., Inc.*
$3.50 5¾ x 9; xiv + 364 *New York*

An introduction to the descriptive morphology of plants, well written and illustrated. Each chapter is followed by a critically selected list of references to the literature.

PLANT PHYSIOLOGY. *Authorized Edition in English, Based on the German Translation of the Sixth Russian Edition and on the Seventh Russian Edition (1914) of the Textbook of Plant Physiology.*
By Vladimir I. Palladin, with additions and editorial notes by Burton E. Livingston.
P. Blakiston's Son and Co.
$4.00 6 x 9; xxxv + 360 *Philadelphia*

The third American edition of a standard botanical text. The chief changes are in the nature of additions to the text and notes by the editor. The continued success of the book is sufficient testimony to its merits.

OBSERVAÇÕES GERAES E CONTRIBUIÇÕES AO ESTUDO DA FLORA E PHYTOPHYSIONOMIA DO BRASIL. I. *Uma Excursão Botanica ao Norte de São Paulo e Regiões Limitrophes dos Estados de Minas e Rio de Janeiro. Realisada de 12 de April a 5 de Maio de 1926.*
By F. C. Hoehne. *Museu Paulista*
—— 9 x 12½; 55 (paper) *São Paulo*

This is a copiously illustrated account of a floristic-ecologic excursion in Brazil.

MORPHOLOGY

GRUNDRISS DER WISSENSCHAFTLICHEN ANATOMIE. *Zum Gebrauch neben jedem Lehrbuch der Anatomie, für Studierende und Ärzte.*
By Wilhelm Lubosch. *Georg Thieme*
M. 18 *Leipzig*
6⅝ x 9½; viii + 292 (paper)

The idea behind this interesting and valuable book is that the student of human anatomy is kept so busy learning the enormous collection of mere facts which he must know, that he has no time to learn, or even to think of, the broad biological significance of anatomy, or its philosophical meaning and relations to other sciences. In reasonable compass and in readable form this book aims to give him this general orientation. It succeeds admirably. Some enterprising American publisher ought to get out an English translation.

THE EMBRYOLOGY OF THE PIG.
By Bradley M. Patten.
P. Blakiston's Son and Co.
$3.50 6 x 9; ix + 323 *Philadelphia*

A text book of mammalian embryology for students of university grade. It is abundantly and very well illustrated. While the account centers about the pig embryo, because of its easy availability for class work, the intention is to use it only as a paradigm for mammalian de-

velopment generally. There is an excellently chosen and rather extensive bibliography, and a detailed index.

ZUR REFORM DER ALLGEMEINEN VERGLEICHENDEN FORMENLEHRE DER TIERE.

By E. Jacobshagen. *Gustav Fischer*
Mk. 4.50 6½ x 9½; 86 (paper) *Jena*

This volume is concerned with a discussion of the methodological and philosophical concepts underlying morphology, particularly homology.

PHYSIOLOGY

L'HERPÈS ET LE ZONA. *"Ectodermoses Neurotropes." Étude Étiologique et Pathogénique.*

By C. Levaditi. *Masson et Cie.*
$1.28 6¼ x 9¼; viii + 388 (paper) *Paris*

This volume represents the report on the nature of the virus of herpes that Levaditi was commissioned to make before the Congress of Dermatology and Syphilology held in Brussels in 1926. So authoritative and extensive a résumé of our knowledge will doubtless be received with great interest by all those workers who are now puzzling over the problems of herpes and its relationships to encephalitis lethargica. In his analysis, Levaditi takes up the infectious nature of herpes, the ways in which it can be transmitted to animals, the properties of the virus, the ways in which it usually gets into the body, the histologic appearances of the experimental lesions, the receptivity of the different tissues, immunity, and its mode of production. He concludes that many persons are carriers and that the virus takes effect when resistance is lowered. Certain strains of the virus of herpes apparently have a strong affinity for the tissues of the central nervous system, but there are many reasons for believing that they are not responsible for encephalitis lethargica. The two viruses are probably related but their elective affinities are different. There are many references to the Continental literature, and a few to American contributions. The book is fairly well illustrated, but there is no index.

MUSCULAR CONTRACTION *and the Reflex Control of Movement.*

By J. F. Fulton.
The Williams & Wilkins Co.
$10.00 6 x 9; xv + 644 *Baltimore*

This is a comprehensive, thorough monograph *de motu animalium*, based largely upon the author's own researches, but with extensive review of the literature. The first part of the book deals with the physiology of the individual skeletal muscle fibre, and the second part with integrated muscular action in bodily movements and postures. The whole is a contribution to physiology of the first rank. The book is extensively illustrated, contains a bibliography of 1066 titles, and author and subject indices.

THE LYMPHOCYTE IN RESISTANCE TO TISSUE GRAFTING, MALIGNANT DISEASE, AND TUBERCULOUS INFECTION. *An Experimental Study. Monographs of The Rockefeller Institute for Medical Research. No. 21.*

By James B. Murphy.
The Rockefeller Institute for Medical Research
$2.00 6¾ x 9⅞; 168 (paper) *New York*

In this monograph Dr. Murphy brings together, in a connected whole, the results of the investigations which have been carried on in his laboratory during

the past fourteen years, on the function of the lymphocyte as a defense mechanism of the organism, particularly with reference to malignant tumors. It is of great service to have this valuable work available in a single volume. It is an important contribution to the cancer problem.

DIE DREI-DRÜSENTHEORIE DER HARNBEREITUNG.
By August Pütter. *Julius Springer*
Rm. 9.60 *Berlin*
6¼ x 9⅝; v + 173 (paper)

The "three glands" of the kidney, according to Pütter's view, are: (a) the "nitrogen glands" of the *tubuli contorti*, (b) the "water glands" of Bowman's capsule of the glomeruli, and (c) the "salt glands" of the thickened shank of Henle's loop. He presents a mass of experimental and observational data, both personal and derived from the literature, in support of the view that by the combined action of these "glands," the known activities of the kidney can be explained.

RECENT ADVANCES IN PHYSIOLOGY. *Second Edition.*
By C. Lovatt Evans.
P. Blakiston's Son and Co.
$3.50 *Philadelphia*
5¼ x 8; xiii + 370

This excellent little book, which was enthusiastically recommended in THE QUARTERLY REVIEW OF BIOLOGY when it appeared, has already passed into a second edition. The chief alterations have to do with thyroxin and insulin. We again commend it to all biologists as a most entertaining and lucid account of present activities in the field of physiology.

ACTIONS AND USES OF THE SALICYLATES AND CINCHOPHEN IN MEDICINE.
By P. J. Hanzlik.
The Williams & Wilkins Co.
$3.50 6 x 9; xiii + 200 *Baltimore*

On account of the large amount of research work that Hanzlik has done on the salicylates he comes well prepared to the discussion of his subject. His book will be of great interest, not only to pharmacologists, but to all those clinicians who are concerned with the problems of treating arthritis. The reviewer, a clinician, found it easy to read it from cover to cover.

DIE HÖCHSTE NERVENTÄTIGKEIT (DAS VERHALTEN) VON TIEREN.
Eine zwanzigjährige Prüfung der objektiven Forschung bedingte Reflexe.
By J. P. Pawlow (Translated by G. Volborth).
J. F. Bergmann
RM. 24 *Munich*
6¾ x 10; xi + 330 (paper)

It is a useful contribution to the literature to have collected in one volume, and in a language more widely known than Russian, the scattered original papers, lectures and addresses of Professor Pawlow on conditioned reflexes and related aspects of the physiology of the central nervous system. The book unfortunately has only three illustrations, and no subject index.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 216.* Containing following articles: *Die Luftcalorimetrie*, by Max Rubner; *Eine Methode der Calorimetrie kleiner Tiere*, by Richard Wagner; *Der Kestnersche Respirationsapparat für kleine Tiere*, by Franz Groebbels; *Die Calorimetrie*, by W. Klein and Marie Steuber;

Graphische Stoffwechselregistrierung, by Erich Leschke; *Die Respirationsapparate für Menschen des Physiologischen Institutes Hamburg*, by Otto Kestner; *Über die Verwendung von Masken zur Bestimmung des respiratorischen Gaswechsels*, by Hermann v. Schroetter.

Urban und Schwarzenberg

Mk. 6 7 x 10; 117 (paper) *Berlin*

It is the first three of the contributions in this number of the Abderhalden handbook which will chiefly interest general biologists. The later sections are for the human physiologist.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 209. Die radioaktiven Substanzen*, by Stefan Meyer. *Bestimmung der Verbrennungswärme und ergänzende thermochemische Messungen*, by A. W. Roth. *Urban und Schwarzenberg*

Mk. 7.80 7 x 10; 153 (paper) *Berlin*

This number of the Abderhalden handbook is chiefly of interest to the biophysicist. The discussion of both radioactive substances and thermochemical measurements is primarily physical in the technical sense.

BIOCHEMISTRY

RECENT ADVANCES IN BIOCHEMISTRY.

By John Pryde.

P. Blakiston's Son and Co.

$3.50 *Philadelphia*

5¼ x 8; viii + 348

This is a companion volume to Lovatt Evans' excellent little treatise in the "Recent Advances" series. While perhaps of smaller general biological interest than that book, it is nevertheless a sound and useful piece of work. The subjects reviewed are: Protein catabolism; amino acids and urea; colloids; nucleo-proteins; carbohydrates; fats; phosphorus compounds; sulphur; vitamins; haemoglobin; specific immunological reactions; and chemotherapy.

DER HEUTIGE STAND DER CHEMOTHERAPEUTISCHEN CARCINOMFORSCHUNG.

By N. Waterman. *Julius Springer*

Rm. 6.60 6¾ x 10; 74 (paper) *Berlin*

A review of the literature with the presentation of original data regarding the biochemistry of malignant tumors, with special reference to their therapeutic treatment with ions of the metals. There is a bibliography covering over two pages.

INTRODUCTION TO PHYSIOLOGICAL CHEMISTRY.

By Meyer Bodansky.

John Wiley and Sons, Inc.

$4.00 5¾ x 9; vii + 440 *New York*

An excellent condensed text, by the associate professor of physiological chemistry in the University of Texas. Abundant bibliographical citations are given in footnotes.

LEHRBUCH DER PHYSIOLOGISCHEN CHEMIE.

By Olof Hammarsten, with the collaboration of S. G. Hedin, J. E. Johansson and T. Thunberg. *J. F. Bergmann*

29.40 RM. *München*

6¾ x 10; viii + 835 (paper)

The eleventh edition of the standard text book of physiological chemistry. The chapter on metabolism and nutrition has been entirely rewritten on a new plan,

while other chapters have been brought up to date.

PRACTICAL COLLOID CHEMISTRY. *By Wolfgang Ostwald, with the collaboration of Dr. P. Wolski and Dr. A. Kuhn. Translated by 1. Newton Kugelmass and Theodore K. Cleveland.* *E. P. Dutton and Co.* $2.25 5 x 7¾; xvi + 191 *New York*

The fourth edition of this widely used laboratory manual, considerably revised, and with fifteen new experiments added.

SEX

SEX IN MAN AND ANIMALS. *By John R. Baker.* *Alfred A. Knopf, Inc.* $3.00 5½ x 8⅝; xvi + 175 *New York*

A brief popular account, for the general reader, of the present status of biological knowledge regarding sex. The topics treated are: The biological significance of sexual reproduction, sex characters and sexual selection; sex chromosomes; sex hormones; abnormalities of sex; hermaphroditism; parthenogenesis; sex ratio; control of sex; sex behavior. The book is well written, but no harm would have been done by *naming* some more of the biologists whose investigations made it possible for Mr. Baker to write this book. After all the investigators who furnish the raw material from which writers of popular science compose their delicious confections are actual persons, lowly though their status be. Who knows but that they might be spurred on to even nobler efforts by a little personal recognition?

[*Editorial Note:* Lest there be any misunderstanding we think it wise to say that the writer of this notice has never worked in the fields of biology discussed by Mr. Baker.]

THEORIES REGARDING THE DETERMINATION OF SEX AND THE POSSIBILITIES OF SEX CONTROL. *By Nils O. Lundell.* *Nils O. Lundell* —— *608 Broadway, Far Rockaway, N. Y.* 6 x 9; 10 (paper)

The author, who is a practising physician graduated from Cornell University Medical College in 1911, claims "that it is possible to examine the maternal and paternal bloods in early pregnancy and tell what the sex of the offspring will be; also that examination of these bloods prior to conception will tell what the sex will be if impregnation takes place and further that we can control the sex when dealing with normal healthy individuals and sex organs."

He then presents an affidavit to the effect that in "over one hundred cases" he "foretold what the sex would be and made no errors." Unfortunately he omits anywhere to state just how the trick is turned.

THE REPRODUCTION OF LIFE. *A Handbook of the Science of Reproduction in Nature and Man.* *By A. J. Cokkinis.* *Wm. Wood and Co.* $3.50 *New York* 5¼ x 8¼; xvi + 287

An excellent elementary account, with abundant illustrations, of the general biology of reproduction in plants and animals including man. There is a refreshing absence of moral precepts. The book is just plain, unadorned biology, stated clearly and in simple language.

HAPPINESS IN MARRIAGE. *By Margaret Sanger.* *Brentano's* $2.00 5¼ x 7½; 231 *New York*

A *vade-mecum* for newlyweds, written

with charm, insight, and a refreshing absence of pseudo-scientific slush by way of rationalization. The sound central idea of this book is that the kind of activity which constitutes the sole reason for a male bee's existence can be made a very pleasant pastime.

SEX HYGIENE. *The Anatomy, Physiology, and Hygiene of the Sex Organs.*
By Julia Kinberg-von Sneidern and Alma Sundquist. Translated by Mary E. Collett.
Henry Holt and Co.
$1.75 5¼ x 8; 114 *New York*

A brief, sensible treatise on the personal hygiene of sex. The Swedish original first appeared fifteen years ago, and has met with success as a supplement to biological texts used in secondary schools.

MAN AND WOMAN. *A Study of Human Secondary Sexual Characters.*
By Havelock Ellis. *A. and C. Black, Ltd.*
10s. 6d. *London*
5½ x 8½; xxiii + 563

The sixth revised edition of a well known treatise. It is a useful work of reference, which fortunately carries no obligation to the reader to agree with all the conclusions.

BIOMETRY

INTERPOLATION.
By J. F. Steffensen.
The Williams & Wilkins Co.
$8.00 6 x 9; ix + 248 *Baltimore*

This is a technical mathematical treatise, which covers with great thoroughness and detail the subjects of interpolation, quadrature, numerical differentiation and integration, etc. It will be found a valuable reference work by the advanced biometrician.

PSYCHOLOGY AND BEHAVIOR

THE ADVENTURES OF A LION FAMILY *and Other Studies of Wild Life in East Africa.*
By A. A. Pienaar. Translated from the Afrikaans by B. and E. D. Lewis.
Longmans, Green and Co., Ltd.
$1.65 4¾ x 7¼; xv + 256 *New York*

A most entertaining book, written by a young Dutch South African. It embodies three stories, based upon his observations in the field as a hunter and amateur naturalist. The bulk of the book is made up of the story of a family group of lions. The second story is unimportant. The last concerns the adventures of a rhinoceros and a hippopotamus, who started an association with each other when they were left as orphans at the same time through the activity of hunters, and fought the battles of life together until one of them was killed by a poisoned spear.

By some this book will be instantly branded as arrant nature-faking. Perhaps it is. But anyhow it is only fair to let the witness be heard. The author says:

> Imagination plays no part in the following sketches of animal life. The writer has simply endeavoured to reproduce the habits and life of the wild creatures which he has learnt to know during the course of many a year. Among wild animals there also exists a kind of spiritual life which often fills the attentive observer with wonder. After a while it becomes possible for him to comprehend their sensations from their outward behaviour.
>
> In the sketch, "The Two Friends," where the action proceeds for a long period and in changing scenes, the writer has incorporated various incidents

in one tale; yet in the smallest particular it rests upon observations that are absolutely true to Nature, and upon personal experiences.

In the "Adventures of a Lion Family" the occurrences—with the exception of parts of the last chapter—are written down almost literally as they happened.

The scenery in which the animals are depicted is in every detail drawn from Nature.

Just a little while before we read this book we waded through a long and preternaturally dull account of an investigation of the habits of an invertebrate that shall be nameless, by a serious, indeed a very serious, student of animal behavior, who had been brought up in the notion that he must never read into the behavior of an animal any anthropopsychism. The net result of this careful investigation was simply to prove that the author was an idiot, and to leave the state of real knowledge of the animal about where it was before. If this kind of painstaking nonsense is to be regarded as science and Pienaar's real insight is to be branded as imagination, God will presently have to take even greater pity on erring mortals than he so far has.

THE MIND OF A GORILLA. *Genetic Psychology Monographs, Vol. II, Nos. 1 and 2, By Robert M. Yerkes.* *Clark University*
$3.00 *Worcester, Mass.*
6 x 9; 193 (paper)

This is an extraordinarily interesting book. It recounts the author's experiences with Congo, a young female gorilla. Her owner, Mr. Ben Burbage, gave every opportunity, at his home in Florida, for the observational and experimental study of her behavior. In some respects this seems to us the best piece of work Yerkes has ever done in his long and distinguished career as a comparative psychologist. At its high points it seems to achieve real insight into the mind of this charming female, who is plainly no fool, but on the contrary, within certain limitations, a highly intelligent creature. Given a parallel set up, in the two important respects that no communication by language was possible, and that the environmental conditions and the experimental demands were totally different from those encountered in the natural course of existence, we suspect that many a stenographer would give less evidence of intelligence, as an experimental subject, than did Congo. He is a dull clod who will not be thrilled by this book. We eagerly await further reports about Congo.

MYTH IN PRIMITIVE PSYCHOLOGY. *By Bronislaw Malinowski.*
W. W. Norton and Co., Inc.
$1.00 $4\frac{1}{4}$ x $6\frac{1}{2}$; 94 *New York*

The distinguished author presents detailed evidence from his wide field experience as an anthropologist, in support of the thesis that:

Myth, as a statement of primeval reality which still lives in present-day life and as a justification by precedent, supplies a retrospective pattern of moral values, sociological order, and magical belief. It is, therefore, neither a mere narrative, nor a form of science, nor a branch of art or history, nor an explanatory tale. It fulfils a function *sui generis* closely connected with the nature of tradition, with the continuity of culture, with the relation between age and youth, and with the human attitude towards the past. The function of myth, briefly, is to strengthen tradition and endow it with a greater value and prestige by tracing it back to a higher, better, more supernatural reality of initial events.

Myth is, therefore, an indispensable ingredient of all culture. It is, as we have seen, constantly regenerated; every historical change creates its mythology, which is, however, but indirectly related to historical fact. Myth is a constant by-product of living faith, which is in need of miracles; of sociological status, which demands precedent; of moral rule, which requires sanction.

LE FONDEMENT PHYSIOLOGIQUE DES INSTINCTS DES SYSTÈMES NUTRITIF, NEUROMUSCULAIRE ET GÉNITAL.

By Bjorg-Caritas Thorlakson.

Les Presses Universitaires de France

20 francs *Paris*

5½ x 9; 393 (paper)

An interesting philosophical essay by an Icelandic author, which attempts to arrive at a rational picture of the biological basis of instincts. His theory is essentially holistic (*sensu* Smuts). It may be put as a formula in this way. The synthesis aptitude (= in part at least appetite) + function + structure is at the same time a morphogenetic and an instinctive-genetic synthesis. The argument is well documented from a rather wide knowledge of general biology and physiology.

ON THE MELODIC RELATIVITY OF TONES. *Psychological Monographs. Vol. XXXV, No. 1.*

By Otto Ortmann. *Psychological Review Co.*

—— *Princeton, N. J.*

6⅝ x 9¾; 47 (paper)

A valuable contribution to the psychology of music. Perhaps the most interesting conclusion, which is supported by sufficiently extensive statistical data, is that the melodic relationship of tones is based upon pitch-proximity, with which it varies directly.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

LES NÉOPLASMES ET LEUR THÉRAPEUTIQUE MÉDICALE.

By Ed. Baronaki. *Norbert Maloine*

12 francs *Paris*

5⅜ x 7½; 137 (paper)

The author of this treatise, who is an honorary surgeon of the *Hôtel-Dieu* at Blois, believes that cancer has its inception in a disturbance of the endocrine balance, and that the way to treat malignancy is by injecting a substance which he calls "Neoplastine," which is a colloidal, "plasmatic" solution containing a mixture, in unspecified proportions, of the salts of calcium, magnesium, phosphorus, potassium and sodium, associated with thyroid and suprarenal extracts. Besides this some rather wonderful "cachets" are exhibited, which are said to contain, again in unspecified proportions, diastatic and tryptic ferments, oxyhemoglobin and lecithin, and soluble salts of lime and soda. According to 20 case histories, given at the end, the treatment leaves little to be desired. But before the work is accepted at its face value it would be well to have an independent investigation of its merits, presuming that Dr. Baronaki is prepared to disclose the details of the composition of his medicines.

RELATIVITY IN MAN AND SOCIETY.

By Arthur F. Bentley.

G. P. Putnam's Sons

$3.00 *New York*

5½ x 8¼; xix + 363

What worries Mr. Bentley is the ambiguity of words, particularly words used in discussions of psychological and sociological matters. For example, he thinks that what the rest of us call "sociology" would be better called "man-society." And since this is the main subject that he wants to talk about he feels it essential to discuss a lot of other words which undeniably get us all into trouble.

Thus: "Let us take a social fact or fact-complex, any one. Take the Volstead Law, federal prohibition of alcoholic drinks. What do we have? A set of words, an enacting clause, many printed

copies. When we have said that, have we said anything?"

To which rhetorical question a joyful shout arises in the Maryland Free State, NO-O-O-O!

The relation of Einstein to all this seems to be precisely that which King Charles' head had to the meditations of Mr. Dick.

THREE LECTURES ON ATOMIC PHYSICS.

By Arnold Sommerfeld. Translated by Henry L. Brose. *E. P. Dutton and Co.*
$1.00 $4\frac{3}{4}$ x $7\frac{1}{4}$; 70 *New York*

This little book has nothing directly to do with biology. The lectures deal with recent developments of the quantum theory. But the biologist nowadays ought at least to have some notion of the extraordinary goings-on in physics, for some of the modes of thinking now current in that science are of a sort with which the biologist has long been familiar (cf. Whitehead for example). In our youth we were not accustomed to meet such statements as the following from the book under review (p. 7), in a technical treatise on physics. "We have a 'phylogenetic principle' for atoms just as much as in biology."

THE NEW SCIENCE OF RADIENDOCRINOLOGY IN ITS RELATION TO REJUVENATION AND THE RELIEF OF COMMON AILMENTS. *Based on the Radiation Technique of Dr. Eugen Steinach of Vienna.*

By One of America's Foremost Radiendocrinologists. *Medical Science Publishing Co.*
$1.00 $4\frac{1}{2}$ x $6\frac{1}{8}$; 64 (paper)

Abrams may be dead but his ions still go marching on. "The Radiendocrinator is an extremely complex apparatus, despite its small size and apparent simplicity of construction. Yet it is not difficult to comprehend the basic principle by which it operates." This is the only description of the apparatus to be found. But truly the basic principle on which it operates is *not* difficult to comprehend. It is that fundamental physical principle, technically known as *gullibility*.

ÉDUCATION, SCIENCE, PATRIE.

By Lucien Poincaré. *Ernest Flammarion*
10 francs *Paris*

$4\frac{1}{2}$ x $7\frac{1}{2}$; 246 (paper)

A posthumous collection of popular essays and public addresses dealing with educational problems and patriotism. It is beautifully written by a master of the French language. But it is dubious whether any useful purpose will be served by the preservation of material of such ephemeral significance.

DER CHRISTLICHE MONISMUS. *Zeitgemässe Betrachtungen über christliche Glaubenswahrheiten.*

By Erich Wasmann. *Herder und Co.*
Mk. 2 *Freiburg*

$4\frac{1}{2}$ x $6\frac{7}{8}$; xii + 105

A pious tract which has nothing to do with myrmecophily or with any other branch of zoology. Its purpose seems to be primarily to strengthen the faith of those who have it, and perhaps snare a sinner here and there and fetch him into the fold. But it has nothing to do with biology. It is a *very* pious book.